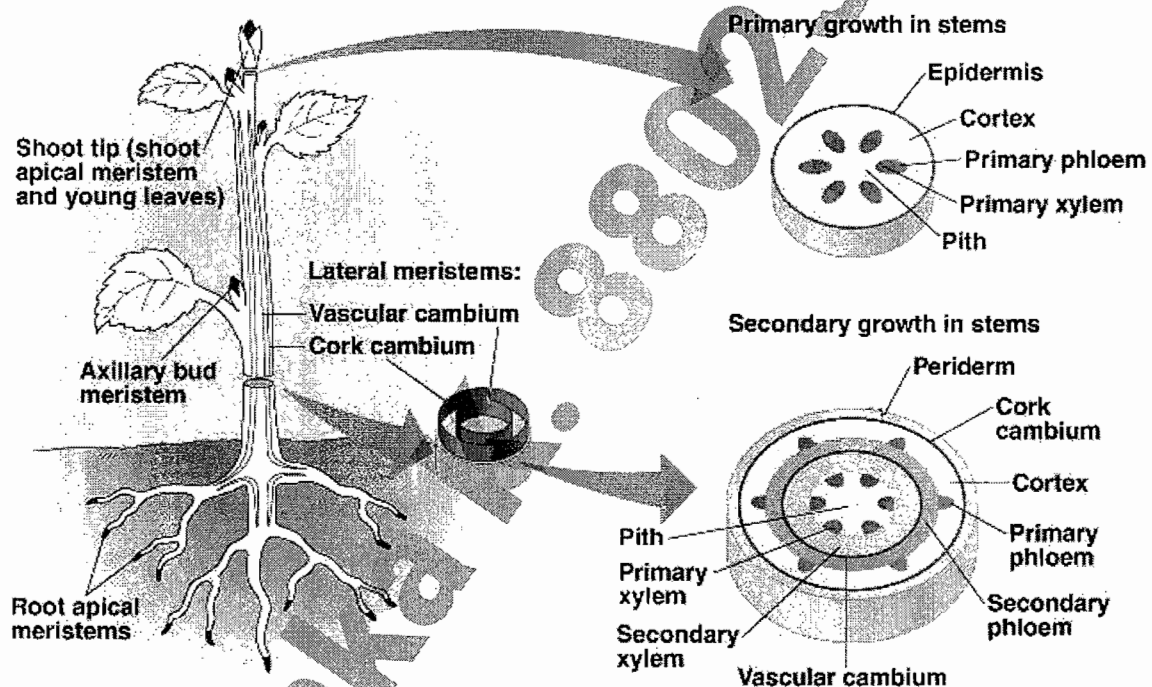


Plant Anatomy



Plant Anatomy

Tissue and tissue systems	4
Tissue and tissue systems: An overview	4
Meristematic tissue.....	4
Characteristics of meristematic cells	5
Classification of meristem	5
Permanent tissue	6
Classification of permanent tissue	6
Simple tissue.....	6
Complex tissue	9
The tissue system	14
Epidermal tissue system	14
Vascular tissue system	15
Ground or fundamental tissue system	17
Anatomy of monocot and dicot roots	19
Primary structure of monocotyledonous root – Maize root	19
Rhizodermis or epiblema	19
Cortex	20
Stele.....	20
Primary structure of dicotyledonous root - Bean root.....	21
Rhizodermis or epiblema	22
Cortex	22
Stele.....	22
Pericycle	23
Vascular system	23
Anatomy of monocot and dicot stems	25
Primary structure of monocot stem - Maize stem	25
Epidermis.....	25
Hypodermis	25
Ground tissue	25
Vascular bundles	26
Phloem	26
Xylem.....	26
Primary structure of dicotyledonous stem - Sunflower stem	27
Epidermis.....	27
Cortex.....	27
Stele.....	28
Pericycle	28
Vascular bundles	28
Pith	29
Anatomical differences between dicot stem and monocot stem	29
Apical Meristems.....	30
The concept of apical meristems	30
Evolution of the concept of apical organization.....	30
Apical Cell Theory.....	30
Histogen Theory.....	31
Tunica-Corpus Theory.....	32
Mantle-core concept	33
The current concept of shoot apex in angiosperms.....	33
Root apex organization	34
The Korper-Kappe Theory.....	35

Stomatal anatomy	36
Introduction to the stomata	36
<i>What Are Stomata?</i>	36
<i>How are the Stomata Distributed?</i>	36
<i>On an Angiosperm Leaf</i>	36
Structure of the stomata	37
<i>Functional Anatomy of the Guard Cells</i>	39
Origin of stoma	39
Types of stoma	44
Functional significance of different stomatal types	48
Trichomes	50
Introduction to trichomes & their various types	50
Occurrence	50
Morphological Categories	51
Glandular trichomes	54
Development of trichomes	55
Functions of trichomes	56
C4 leaf (Kranz type) Anatomy	58
The essentials of C4 leaf (Kranz type) Anatomy	58
The construction of a C4 leaf	59
Functional importance of Kranz Anatomy	60
Is Kranz Anatomy Universal in C4 Plants?	62
Xylem and phloem differentiation	63
A general account of differentiation	63
<i>Differentiation in Plants</i>	63
<i>Stability of Differentiation</i>	64
<i>Stages of Differentiation</i>	64
Xylogenesis	67
<i>Microanatomical outline of the process</i>	68
<i>The Events in Xylogenesis</i>	68
Phloem Differentiation	71
<i>Microanatomical outline of the process</i>	73
Secondary growth in stem and wood anatomy	75
Vascular cambium	75
<i>The cells of the vascular cambium</i>	75
Formation of secondary xylem and secondary phloem	77
Secondary Growth in Monocots	80
Secondary growth in cortex	81
Wood anatomy	84
<i>Axial System of the Wood</i>	85
<i>The Radial System of Wood</i>	86
<i>Ring porous and Diffuse porous wood</i>	87
<i>Annual Rings in Wood</i>	89
<i>Heart Wood and Sap Wood</i>	90
Appendix: Methods of wood sectioning	91
Anomalous Secondary Growth	92
<i>Reasons for Anomaly in Secondary Growth</i>	93
<i>The Ecological Types of Anomalous Secondary Growth</i>	93
The Types of Anomalous Secondary Growth Based on Origin	94
<i>Anomalous Position of Cambium</i>	94
<i>Abnormal behaviour of normally placed cambium</i>	94
<i>Accessory Cambium Formation and its Activity</i>	96
<i>Extrastelar Cambium</i>	96
<i>Secondary development in the monocots</i>	96
Illustrations on anomalous secondary growth	97

Tissue and tissue systems

Plant anatomy (*Ana* = as under, *tamnein* = to cut) is the study of internal structure and organization of plants, especially of their parts by means of dissection and microscopic examination. The simple type of plant body is unicellular. In such forms, the single cell performs all the vital functions of life. It grows, prepares food, undergoes metabolism, reproduces and completes its span of life. The progressive evolution in plants has resulted in increasing complexity of structures. In higher plants, root, stem, leaves and flowers carry out different functions. Due to these divisions of labour, the cells of the plant are differentiated to form different tissues.

Tissue and tissue systems: An overview

The study of internal structure of plants reveals many types of tissues. Morphologically, a tissue is a group of cells, which are similar in origin, form and function. Physiologically, a tissue is composed of dissimilar cells that perform a common function, for example, phloem elements and food conduction respectively. The cells form various kinds of tissues. Two or more types of tissues form tissue systems. Different tissue systems form the organs. Each tissue carries out a specific function. Tissue can be classified into two types –

1. Meristematic tissue
2. Permanent tissue

Meristematic tissue

A meristematic tissue (meristos = divisible) is a group of identical cells that are in a continuous state of division. Some cells produced by meristematic tissue stop dividing and acquire certain changes to become permanent tissues of the plant. This change from meristematic to permanent tissue is called differentiation. The

remaining cells in the meristem retain their meristematic activity. Meristematic cells are self-perpetuating.

Characteristics of meristematic cells

The meristematic cells may be round, oval, polygonal or rectangular in shape. They are closely arranged without intercellular spaces. They have dense cytoplasm with large nucleus. They have smaller vacuoles, which are scattered throughout the cytoplasm. Their cell walls are thin, elastic and made up of cellulose.

Classification of meristem

Based on its position, the meristem is divided into three types - apical meristem, intercalary meristem and lateral meristem.

Apical meristem

Apical meristem is found at the tips of roots, stem and branches. It is responsible for increase in length of plant. It is divided into three zones - protoderm, procambium and ground meristem. Protoderm gives rise to epidermal tissue; procambium gives rise to primary vascular tissues and ground meristem gives rise to cortex and pith.

Intercalary meristem

It is present in the nodal region and is prominently found in monocotyledons, eg. grasses. As the name indicates, it is present in between the permanent tissues. It is derived from the apical meristem and is responsible for the elongation of internodes.

Lateral meristem

The meristem that is present along the longitudinal axis of stem and root is called lateral meristem. Vascular cambium and cork cambium (phellogen) are examples for lateral meristem. It produces, secondary permanent tissues, which result in the thickening of stem and root.

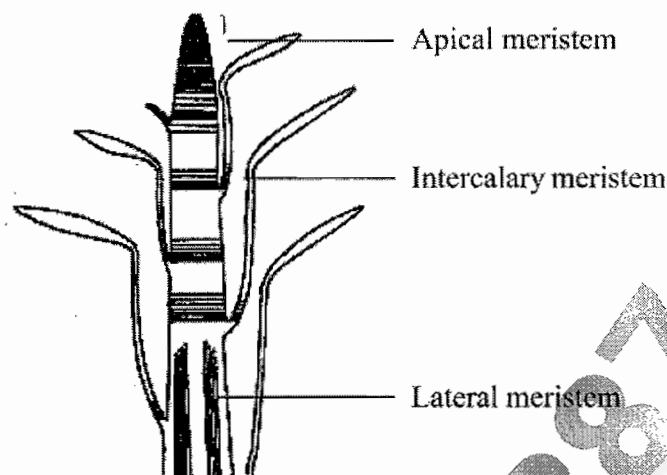


Figure: L.S of shoot - showing the positions of meristems

Permanent tissue

The cells, which are formed by apical meristem, are differentiated into different types of permanent tissues. These tissues have lost the power of dividing either permanently or temporarily.

Classification of permanent tissue

Based on the constituent cells, the permanent tissue is classified into two types - simple tissue and complex tissue.

Simple tissue

A tissue with the cells of similar structure and function is called simple tissue. It is of three types - parenchyma, collenchyma and sclerenchyma.

Parenchyma

It is generally present in all organs of the plant. It constitutes the ground tissue in a plant. Parenchyma is the precursor of all the other tissues. Parenchyma is a living tissue and made up of thin walled cells. The cell wall is made up of cellulose. Parenchyma cells may be oval, spherical, rectangular, cylindrical or stellate. The cells are usually polyhedral with 10-12 facets. Parenchyma is of different types and some of them are discussed as follows.

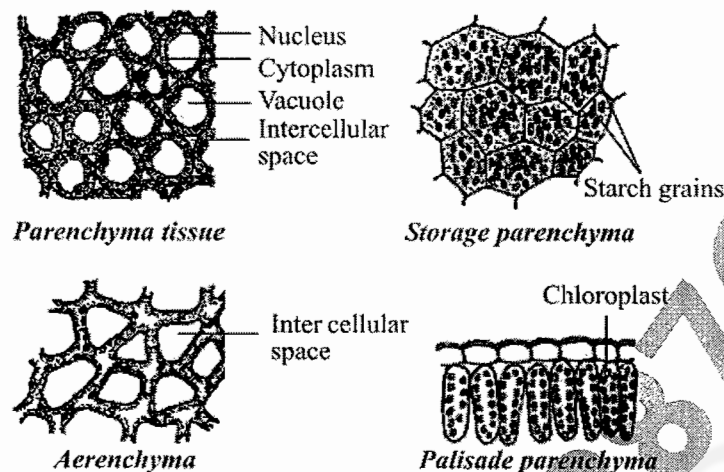


Figure: Types of parenchyma

In water plants, the parenchyma found in the cortex region possesses well-developed large intercellular spaces called air spaces. This air filled parenchyma tissue is called aerenchyma. It helps the plant to float in water, eg. *Nymphaea* and *Hydrilla*. The parenchyma cells that are stored with starch grains are called storage parenchyma, eg. stem and root tubers. In the petioles of banana and *Carina*, star shaped parenchyma cells are found. These cells are called stellate parenchyma. In green parts of the plants, the parenchymatous cells have chloroplasts. These cells are called chlorenchyma. Its important function is photosynthesis.

Collenchyma

Collenchyma generally occurs in the dicot stems in two or more layers below the epidermis. These layers constitute the hypodermis. It is absent in the roots of land plants. It also occurs in petiole and pedicel. It gives strength to young organs. Collenchyma is a living tissue. It consists of more or less elongated cells which are polygonal in cross section. The cell wall is unevenly thickened. The thickening is confined to the corners of the cells. Besides cellulose, the cell wall contains high amounts of hemicelluloses and pectin.

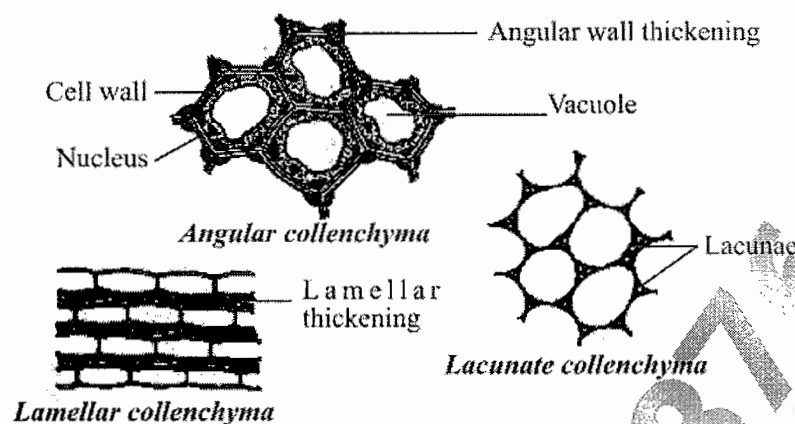


Figure: Types of collenchyma

Collenchyma may contain chloroplasts and carry out photosynthesis. Collenchyma is divided into three types - lamellar, angular and lacunate collenchyma.

In the hypodermis of *Helianthus*, only the tangential walls of collenchyma are thickened and the radial walls are devoid of thickening. This type of collenchyma is called lamellar collenchyma. In the hypodermis of *Datura* and *Nicotiana*, the cell walls of collenchyma are thickened at their angles. This type is called angular collenchyma. In the hypodermis of *Ipomoea*, the cell wall thickening materials are deposited on the walls bordering the intercellular spaces. This type is called lacunate collenchyma.

Sclerenchyma

Sclerenchyma is a dead tissue. The cells have lignified secondary walls. They lack protoplasts. On the basis of origin, structure and function, sclerenchyma is divided into two types - sclereids and fibres. The sclereids are different from fibres in the following respects. Sclereids are shorter whereas fibres are longer. Sclereids possess numerous pits as compared to the fibres.

Sclereids

Sclereids are dead cells. They vary greatly in shape and thickness. The cell wall is very thick due to lignification. Lumen is very much reduced. The pits may be

simple or branched. Usually sclereids are isodiametric, but in some plants they are elongated. They are responsible for the rigidity of the seed-coat. The isodiametric sclereids are called brachy-sclereids (stone cells). They are found in bark, pith, cortex, hard endocarp and fleshy portions of some fruits, eg. pulp of *Pyrus*.

Elongated rod shaped sclereids are called macrosclereids (rod cells). They are found in the outer seed coat. eg. *Crotalaria*. The rod shaped sclereids with dilated ends are called osteosclereids (bone cells), eg. seed coat of *Pisum*.

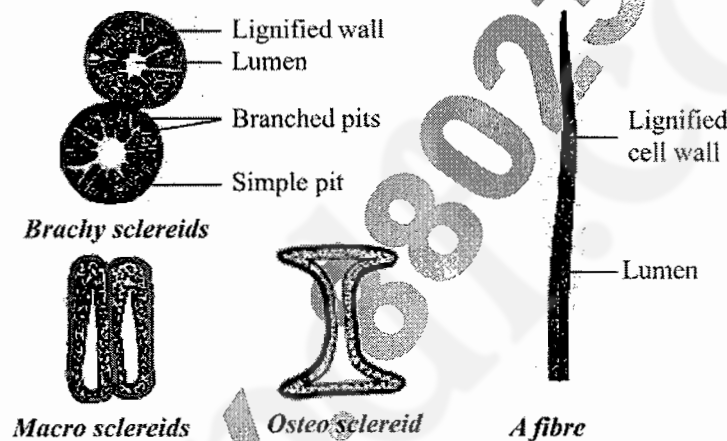


Figure: Types of sclerenchyma

Fibres

Fibre cells are dead cells. They are very long and narrow with pointed ends. In transverse section, the fibres are polygonal with narrow lumen. The secondary wall is evenly thickened with lignin. It possesses simple pits. Fibres are supporting tissues. They provide mechanical strength to the plants and protect them from the strong winds. The fibres that are found in the seed coat of some seeds are called surface fibres. eg. cotton.

Complex tissue

A tissue that consists of several kinds of cells but all of them function together as a single unit is called complex tissue. It is of two types' xylem and phloem.

Xylem

Xylem (Greek word 'xylos' = wood) is a complex tissue that is mainly responsible for the conduction of water and mineral salts from roots to other parts of the plant. The xylem, which is derived from procambium is called primary xylem and the xylem, which is derived from vascular cambium, is called secondary xylem. Earlier formed xylem elements are called protoxylem, whereas the latter formed xylem elements are called metaxylem. Xylem is made up of four kinds of cells – tracheids, vessels or tracheae, xylem fibres and xylem parenchyma.

Tracheids

Tracheids are elongated with blunt ends. Its lumen is broader than that of fibres. Their secondary wall is lignified. In cross section, the tracheids appear polygonal and thick walled. The pits are simple or bordered. There are different types of cell wall thickening due to deposition of secondary wall substances. They are annular (ring like), spiral (spring like), scalariform (ladder like), reticulate (net like) and pitted (uniformly thick except at pits). Tracheids are imperforate cells with bordered pits on their end walls. They are arranged one above the other. Tracheids are chief water conducting elements in gymnosperms and pteridophytes. Here, the conduction of water and mineral salts takes place through the bordered pits. They also offer mechanical support to the plants.

Vessels or Tracheae

Vessels are perforated at the end walls. Its lumen is wider than that of tracheids. The perforated plates at the end wall separate the vessels. They occur parallel to the long axis of the plant. Due to dissolution of entire end wall, a single pore is formed at the perforation plate. It is called simple perforation plate eg. *Mangifera*. If the perforation plate has many pores, then it is called multiple perforation plate e.g. *Liriodendron*.

The secondary wall thickenings of vessels are annular, spiral, scalariform, reticulate, or pitted as in tracheids. Vessels are chief water conducting elements

in angiosperms and they are absent in pteridophytes and gymnosperms. However, in *Gnetum* of gymnosperms, vessels occur. The main function of vessel is conduction of water and minerals. It also offers mechanical strength to the plant.

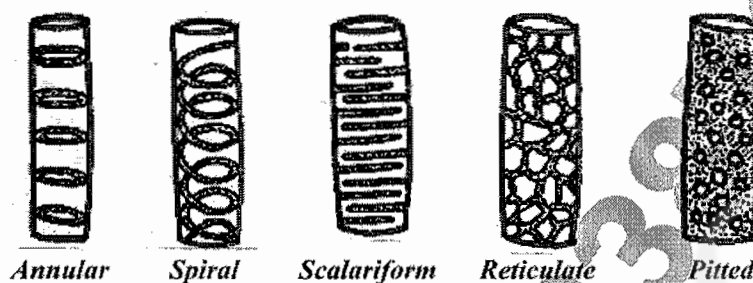


Figure: Types of secondary thickening in Xylem

Xylem fibres

The fibres of sclerenchyma associated with the xylem are known as xylem fibres. They give additional mechanical support to the plant body. They are present both in primary and secondary xylem. Xylem fibres are dead cells and have lignified walls with narrow lumen. Xylem fibres are also called libriform fibres.

Xylem parenchyma

The parenchyma cells associated with the xylem are known as xylem parenchyma. Xylem parenchyma is the only living tissue amongst the constituents of xylem. The cell wall is thin and made up of cellulose. The xylem parenchyma cells store food reserves in the form of starch and fat. They also assist in conduction of water.

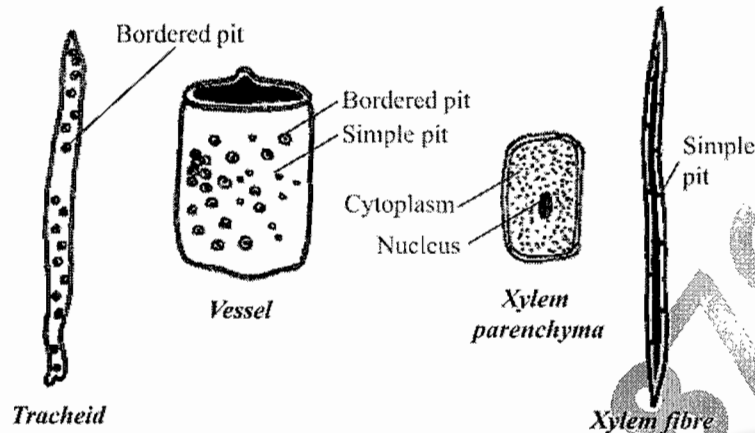


Figure: Types of Xylem Cells

Phloem

Like xylem, phloem is also a complex tissue. It conducts food materials to various parts of the plant. The phloem elements which are formed from the procambium of apical meristem are called primary phloem. The phloem elements which are produced by the vascular cambium are called secondary phloem. The primary phloem elements that develop first from the procambium are smaller in size called the proto phloem, whereas those develop later are larger in size called metaphloem. The protophloem is short lived. It is crushed by the developing metaphloem.

Phloem is composed of four kinds of cells: sieve elements, companion cells, phloem parenchyma and phloem fibres. Companion cells are present only in angiosperms. Companion cells are absent in pteridophytes and gymnosperms. Phloem fibres are absent in the primary phloem of most of the angiosperms. But they are usually present in the secondary phloem.

Sieve elements

Sieve elements are the conducting elements of the phloem. They have thick primary walls. Their end walls are transverse or oblique. The end wall contains a number of pores and it looks like a sieve. So it is called a sieve plate. The sieve elements are arranged one above the other and form vertical sieve tubes. In

matured sieve tube, nucleus is absent. It contains a lining layer of cytoplasm. This is an important feature of sieve elements. A special protein called slime body is seen in it. The conduction of food material takes place through cytoplasmic strands. They are distinguished into sieve cells and sieve tubes. Sieve cells occur in pteridophytes and gymnosperms, while sieve tubes occur in angiosperms.

Sieve cells have sieve areas on their lateral walls only and are not arranged one above the other in linear rows. They are not associated with companion cells. Sieve tubes are arranged one above the other in linear rows and have sieve plates on their end walls. They are associated with the companion cells. In mature sieve elements, sometimes the pores in the sieve plate are blocked by a substance called callose.

Companion cells

The thin-walled, elongated, specialised parenchyma cells, which are associated with the sieve elements, are called companion cells. In contrast to sieve elements, the companion cells have cytoplasm and a prominent nucleus. They are connected to, the sieve tubes through pits found in the lateral walls. The companion cells are present only in angiosperms and absent in gymnosperms and pteridophytes. They assist the sieve tubes in the conduction of food materials, |

Phloem parenchyma

The parenchyma cells associated with the phloem are called phloem parenchyma. These are living cells. They store starch and fats. They also contain resins and tannins in some plants. They are present in all, pteridophytes, gymnosperms and dicots. In monocots, usually phloem parenchyma is absent.

Phloem fibres

The fibres of sclerenchyma associated with phloem are called phloem fibres or bast fibres. They are narrow, vertically elongated cells with very thick walls and a small lumen (the cell cavity). Among the four kinds of phloem elements, phloem fibres are the only dead tissue. These are the strengthening and supporting cells.

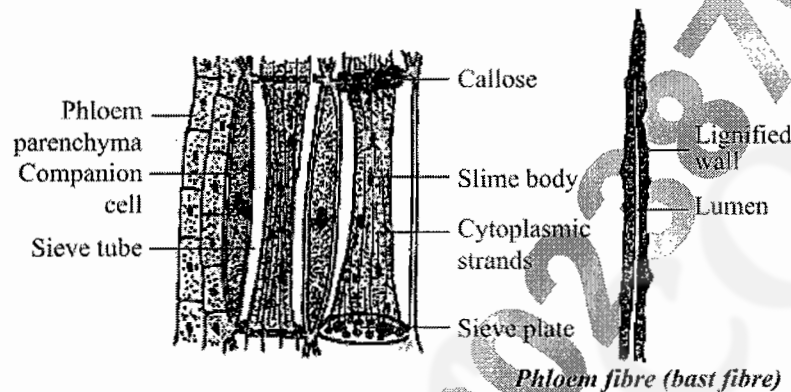


Figure: Phloem Tissue

The tissue system

A group of tissues performing a similar function irrespective of its position in the plant body is called a tissue system. In 1875, Sachs recognized three tissue systems in the plants. They are epidermal tissue system, vascular tissue system and fundamental tissue system.

Epidermal tissue system

Epidermal tissue system is the outermost covering of plants. It consists of epidermis, stomata and epidermal outgrowths. Epidermis is generally composed of single layer of parenchymatous cells compactly arranged without intercellular spaces. But it is interrupted by stomata. In leaves some specialized cells which surround the stomata are called the guard cells. Chloroplasts are present only in the guard cells of the epidermis. Other epidermal cells usually do not have chloroplasts. The outer wall of epidermis is usually covered by cuticle.

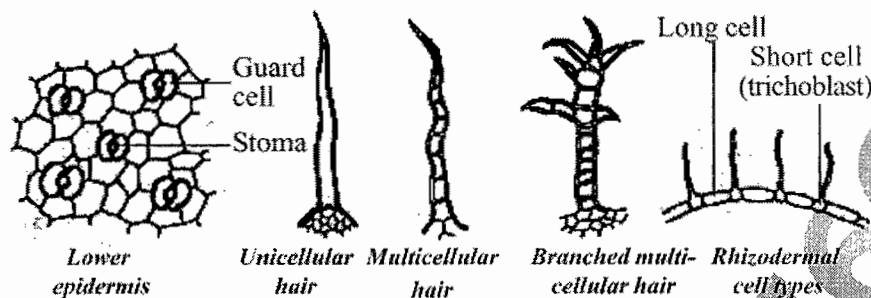


Figure: Epidermal Tissue System

Stoma is a minute pore surrounded by two guard cells. The stomata occur mainly in the epidermis of leaves. In some plants such as sugarcane, the guard cells are bounded by some special cells. They are distinct from other epidermal cells. These cells are called subsidiary or accessory cells. Trichomes and root hairs are some epidermal outgrowths. The unicellular or multicellular appendages that originate from the epidermal cells are called trichomes. Trichomes may be branched or unbranched. Rhizodermis has two types of epidermal cells - long cells and short cells. The short cells are called trichoblasts. Root hairs are produced from these trichoblasts.

Functions of epidermal tissue system

1. This tissue system in the shoot checks excessive loss of water due to the presence of cuticle.
2. Epidermis protects the underlying tissues.
3. Stomata involve in transpiration and gaseous exchange.
4. Trichomes are also helpful in the dispersal of seeds and fruits.
5. Root hairs absorb water and mineral salts from the soil.

Vascular tissue system

The vascular tissue system consists of xylem and phloem. The elements of xylem and phloem are always organized in groups. They are called vascular bundles. In dicot stem, the vascular bundle consists of cambial tissue in between xylem and phloem. Such vascular bundle is called open vascular bundle. In monocot stem,

cambium is absent in the vascular bundle, hence it is known as closed vascular bundle.

In roots, xylem and phloem are arranged in an alternate manner on different radii. It is called radial arrangement. In stems and leaves, xylem and phloem are arranged at the same radius and form a vascular bundle together. Such vascular bundle is called conjoint vascular bundle. Depending upon the mutual relationship of xylem and phloem, conjoint vascular bundles are divided into three types. They are collateral bicollateral and concentric.

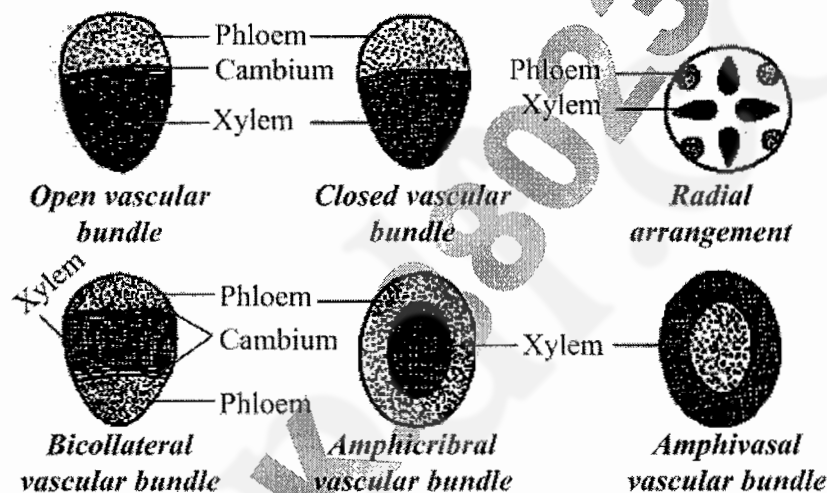


Figure: Vascular tissue system

If xylem and phloem in a vascular bundle are arranged along the same radius with phloem towards the outside, such vascular bundle is called collateral vascular bundle. If phloem occurs on both the outer and inner sides of xylem, the bundle is called bicollateral. Bicollateral vascular bundles are most typically seen in Cucurbitaceae.

The bundle in which either phloem surrounds the xylem or xylem surrounds the phloem completely is known as concentric vascular bundle. This is of two types amphicribral and amphivasal. In amphicribral concentric vascular bundles, the phloem completely surrounds the xylem. eg. *Polypodium*. In amphivasal concentric vascular bundles, the xylem completely surrounds the phloem, eg.

Acorns. In roots, protoxylem vessels are present towards the periphery and the metaxylem vessels towards the centre. This arrangement of xylem is called exarch. In stem, protoxylem vessels are towards the centre, while metaxylem towards the periphery. This condition is known as endarch.

Ground or fundamental tissue system

The ground or fundamental tissue system constitutes the main body of the plants.

It includes all the tissues except epidermis and vascular bundles.

In monocot stem, ground tissue system is a continuous mass of parenchymatous tissue in which, vascular bundles are found scattered. Here ground tissue is not differentiated into cortex, endodermis, pericycle and pith.

Generally in dicot stem, ground tissue system is differentiated into three zones - cortex, pericycle and pith.

The cortex occurs between the epidermis and pericycle. Cortex may be a few to many layers in thickness. In most cases, cortex is made up of parenchyma tissues. Intercellular spaces may or may not be present. Cortical cells may contain non-living inclusions like starch grains, oils, tannins and crystal.

In the leaves, the ground tissue consists of chlorenchyma tissues. This region is called mesophyll.

The inner most layer of the cortex is called endodermis. Generally endodermis is made up of barrel shaped parenchyma cells. These cells are arranged in a single layer without intercellular spaces.

Pericycle occurs between the endodermis and the vascular bundles. It is generally made up of parenchyma cells. Lateral roots originate from the pericycle. Thus their origin is endogenous. The central part of the ground tissue is known as pith or medulla. Generally this is made up of thin walled

parenchyma cells which may be with or without intercellular spaces. The cells in the pith generally store starch, fatty substances, tannins, phenols, calcium oxalate crystals, etc.

Anatomy of monocot and dicot roots

The embryo develops into an adult plant with roots, stem and leaves due to the activity of the apical meristem. A mature plant has three kinds of tissue systems - the dermal, the fundamental and the vascular system.

The dermal system includes the epidermis, which is the primary outer protective covering of the plant body. The periderm is another protective tissue that supplants the epidermis in the roots and stems that undergo secondary growth. The fundamental tissue system includes tissues that form the ground substance of the plant in which other permanent tissues are found embedded. Parenchyma, collenchyma and sclerenchyma are the main ground tissues. The vascular system contains the two conducting tissues, the phloem and xylem. In different parts of the plants, the various tissues are distributed in characteristic patterns. This is best understood by studying their internal structure by cutting sections (transverse or longitudinal or both) of the part to be studied.

Primary structure of monocotyledonous root – Maize root

The internal structure of the monocot roots shows the following tissue systems from the periphery to the centre. They are epiblema or rhizodermis, cortex and stele.

Rhizodermis or epiblema

It is the outermost layer of the root. It consists of a single row of thin-walled parenchymatous cells without any intercellular space. Stomata and cuticle are absent in the rhizodermis. Root hairs that are found in the rhizodermis are

always unicellular. They absorb water and mineral salts from the soil. Root hairs are generally short lived. The main function of rhizodermis is protection of the inner tissues.

Cortex

The cortex is homogenous, i.e. the cortex is made up of only one type of tissue called parenchyma. It consists of many layers of thin-walled parenchyma cells with lot of intercellular spaces. The function of cortical cells is storage. Cortical cells are generally oval or rounded in shape. Chloroplasts are absent in the cortical cells, but they store starch. The cells are living and possess leucoplasts. The inner most layer of the cortex is endodermis. It is composed of single layer of barrel shaped parenchymatous cells. This forms a complete ring around the stele. There is a band like structure made of suberin present in the radial and transverse walls of the endodermal cells. They are called Casparian strips named after Casparay who first noted the strips.

The endodermal cells, which are opposite to the protoxylem elements, are thin-walled without casparian strips. These cells are called passage cells. Their function is to transport water and dissolved salts from the cortex to the xylem. Water cannot pass through other endodermal cells due to casparian strips. The main function of casparian strips in the endodermal cells is to prevent the re-entry of water into the cortex once water entered the xylem tissue.

Stele

All the tissues inside the endodermis comprise the stele. This includes pericycle, vascular system and pith.

Pericycle

Pericycle is the outermost layer of the stele and lies inner to the endodermis. It consists of a single layer of parenchymatous cells.

Vascular System

Vascular tissues are seen in radial arrangement. The number of protoxylem groups is many. This arrangement of xylem is called polyarch. Xylem is an exarch condition. The tissue, which is present between the xylem and the phloem, is called conjunctive tissue. In maize, the conjunctive tissue is made up of sclerenchymatous tissue.

Pith

The central portion is occupied by a large pith. it consists of thinwalled parenchyma cells with intercellular spaces. These cells are filled with abundant starch grains.

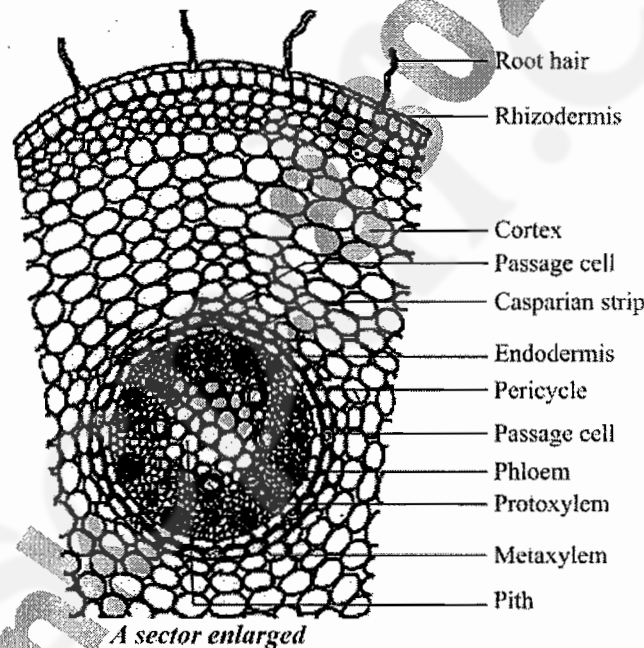


Figure: TS through Maize root

Primary structure of dicotyledonous root - Bean root

The transverse section of the dicot root (Bean) shows the following plan of arrangement of tissues from the periphery to the centre.

Rhizodermis or epiblema

The outermost layer of the root is known as rhizodermis. It is made up of a single layer of parenchyma cells which are arranged compactly without intercellular spaces. It is devoid of stomata and cuticle. Root hair is always single celled. It absorbs water and mineral salts from the soil. The chief function of rhizodermis is protection.

Cortex

Cortex consists of only parenchyma cells. These cells are loosely arranged with intercellular spaces to make gaseous exchange easier. These cells may store food reserves. The cells are oval or rounded in shape. Sometimes they are polygonal due to mutual pressure. Though chloroplasts are absent in the cortical cells, starch grains are stored in them. The cells also possess leucoplasts.

The inner most layer of the cortex is endodermis. Endodermis is made up of single layer of barrel shaped parenchymatous cells. Stele is completely surrounded by the endodermis. The radial and the inner tangential walls of endodermal cells are thickened with suberin. This thickening was first noted by Casparay. So these thickenings are called Casparian's strips. But these casparian strips are absent in the endodermal cells which are located opposite to the protoxylem elements. These thin-walled cells without casparian strips are called passage cells. Through which water and mineral salts are conducted from the cortex to the xylem elements. Water cannot pass through other endodermal cells due to the presence of casparian thickenings.

Stele

All the tissues present inside endodermis comprise the stele. It includes pericycle and vascular system.

Pericycle

Pericycle is generally a single layer of parenchymatous cells found inner to the endodermis. It is the outermost layer of the stele. Lateral roots originate from the pericycle. Thus, the lateral roots are endogenous in origin.

Vascular system

Vascular tissues are in radial arrangement. The tissue by which xylem and phloem are separated is called conjunctive tissue. In bean, the conjunctive tissue is composed of parenchymatous tissue. Xylem is in exarch condition. The number of protoxylem points is four and so the xylem is called tetrarch. Each phloem patch consists of sieve tubes, companion cells and phloem parenchyma. Metaxylem vessels are generally polygonal in shape. But in monocot roots they are circular.

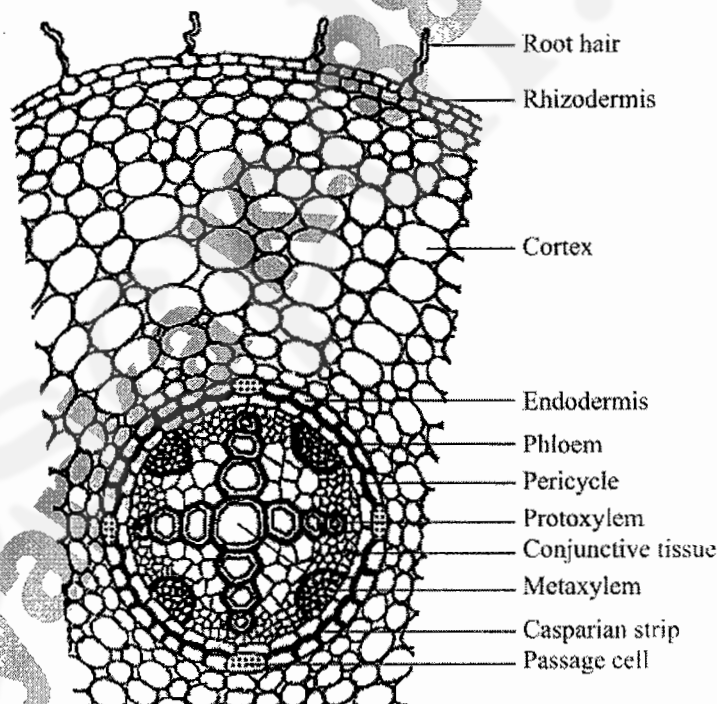


Figure: TS through Bean Root

Monocot roots	Dicot roots
1. Xylem is polyarch.	1. Xylem is usually tetrarch.
2. Pith is usually large at the centre	2. Pith is usually absent.
3. Metaxylem vessels are generally circular in cross section.	3. Metaxylem vessels are generally polygonal in cross section.
4. Conjunctive tissue is sclerenchymatous in Maize.	4. Conjunctive tissue is usually parenchymatous.
5. There is no secondary growth.	5. Secondary growth is generally present.

Figure: Difference between Monocot and Dicot Roots

Anatomy of monocot and dicot stems

Primary structure of monocot stem - Maize stem

The outline of the maize stem in transverse section is more or less circular. Internal structure of monocotyledonous stem reveals epidermis, hypodermis, ground tissue and vascular bundles.

Epidermis

It is the outermost layer of the stem. It is made up of single layer of tightly packed parenchymatous cells. Their outer walls are covered with thick cuticle. The continuity of this layer may be broken here and there by the presence of a few stomata. There are no epidermal outgrowths.

Hypodermis

A few layers of sclerenchymatous cells lying below the epidermis constitute the hypodermis. This layer gives mechanical strength to the plant. It is interrupted here and there by chlorenchyma cells.

Ground tissue

There is no distinction into cortex, endodermis, pericycle and pith. The entire mass of parenchymatous cells lying inner to the hypodermis forms the ground tissue. The cell wall is made up of cellulose. The cells contain reserve food material like starch. The cells of the ground tissue next to the hypodermis are smaller in size, polygonal in shape and compactly arranged. Towards the centre, the cells are loosely arranged, rounded in shape and bigger in size. The vascular bundles lie embedded in this tissue. The ground tissue stores food and performs gaseous exchange.

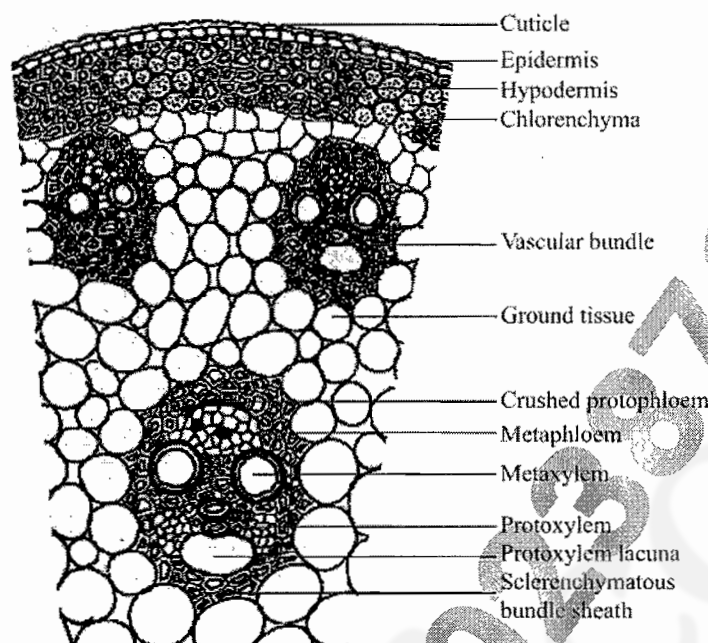


Figure: TS through a sector of Maize stem

Vascular bundles

Vascular bundles are scattered in the parenchymatous ground tissue. Each vascular bundle is surrounded by a sheath of sclerenchymatous fibres called bundle sheath. The vascular bundles are conjoint, collateral, endarch and closed. Vascular bundles are numerous, small and closely arranged in the peripheral portion. Towards the centre, the bundles are comparatively large in size and loosely arranged. Vascular bundles are skull shaped.

Phloem

The phloem in the monocot stem consists of sieve tubes and companion cells. Phloem parenchyma and phloem fibres are absent. It can be distinguished into an outer crushed protophloem and an inner metaphloem.

Xylem

Xylem vessels are arranged in the form of the letter 'Y'. The two metaxylem vessels are located at the upper two arms and one or two protoxylem vessels at the base. In a mature bundle, the lowest protoxylem disintegrates and forms a cavity known as protoxylem lacuna.

Primary structure of dicotyledonous stem - Sunflower stem

Internal structure of dicotyledonous stem reveals epidermis, cortex and stele.

Epidermis

It is protective in function and forms the outermost layer of the stem. It is a single layer of parenchymatous rectangular cells. The cells are compactly arranged without intercellular spaces. The outer walls of the epidermal cells have a layer called cuticle.

Epidermal cells are living. Chloroplasts are usually absent. A large number of multicellular hairs occur on the epidermis.

Cortex

Cortex lies below the epidermis. The cortex is differentiated into three zones. Below the epidermis, there are a few layers of collenchyma cells. This zone is called hypodermis. It gives mechanical strength to the stem. These cells are living and thickened at the corners. Inner to the hypodermis, a few layers of chlorenchyma cells are present with conspicuous intercellular spaces. This region performs photosynthesis. Some resin ducts also occur here. The third zone is made up of parenchyma cells. These cells store food materials.

The innermost layer of the cortex is called endodermis. The cells of this layer are barrel shaped and arranged compactly without intercellular spaces. Since starch grains are abundant in these cells, this layer is also known as starch sheath. This layer is morphologically homologous to the endodermis found in the root. In most of the dicot stems, endodermis with Casparian strips is not developed.

Stele

The central part of the stem inner to the endodermis is known as stele. It consists of pericycle, vascular bundles and pith. In dicot stem, vascular bundles are arranged in a ring around the pith. This type of stele is called eustele.

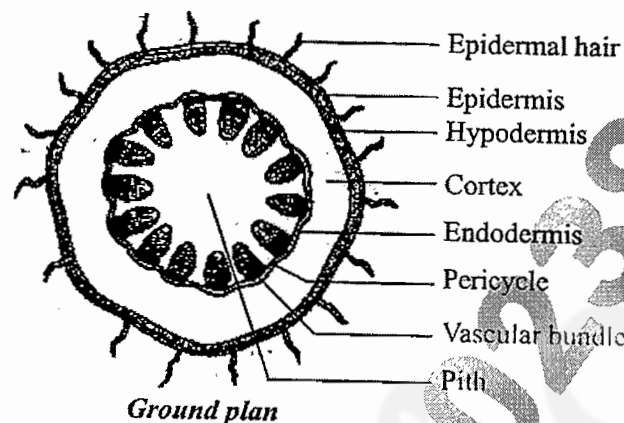


Figure: Ground plan of Sunflower Stem

Pericycle

Pericycle is the layers of cells that occur between the endodermis and vascular bundles. In the stem of sunflower (*Helianthus*), a few layers of sclerenchyma cells occur in patches outside the phloem in each vascular bundle. This patch of sclerenchyma cells is called bundle cap or hard bast. The bundle caps and the parenchyma cells between them constitute the pericycle in the stem of sunflower.

Vascular bundles

The vascular bundles consist of xylem, phloem and cambium. Xylem and phloem in the stem occur together and form the vascular bundles.

These vascular bundles are wedge shaped. They are arranged in the form of a ring. Each vascular bundle is conjoint, collateral, open and endarch.

Phloem

Primary phloem lies towards the periphery. It consists of protophloem and metaphloem. Phloem consists of sieve tubes, companion cells and phloem

parenchyma. Phloem fibres are absent in the primary phloem. Phloem conducts organic food materials from the leaves to other parts of the plant body.

Cambium

Cambium consists of brick shaped and thin walled meristematic cells. It is two to three layers in thickness. These cells are capable of forming new cells during secondary growth.

Xylem

Xylem consists of xylem fibres, xylem parenchyma, vessels and tracheids. Vessels are thick walled and arranged in a few rows. Xylem conducts water and minerals from the root to the other parts of the plant body.

Pith

The large central portion of the stem is called pith. It is composed of parenchyma cells with intercellular spaces. The pith is also known as medulla. The pith extends between the vascular bundles. These extensions of the pith between the vascular bundles are called primary pith rays or primary medullary rays. Function of the pith is storage of food. Anatomical differences between dicot stem and monocot stem

Dicot stem	Monocot stem
<ul style="list-style-type: none"> Hypodermis is made up of collenchymatous cells. Ground tissue is differentiated into cortex, endodermis, pericycle and pith. Starch sheath is present Pith is present Pericycle is present Medullary rays are present Vascular bundles are open. Vascular bundles are arranged in a ring Bundle cap is present Protoxylem lacuna is absent Phloem parenchyma is present. 	<ul style="list-style-type: none"> Hypodermis is made up of sclerenchymatous cells. Ground tissue is not differentiated, but it is a continuous mass of parenchyma. Starch sheath is absent Pith is absent Pericycle is absent. Medullary rays are absent. Vascular bundles are closed Vascular bundles are scattered in the ground tissue Bundle sheath is present Protoxylem lacuna is present Phloem parenchyma is absent.

Apical Meristems

The concept of apical meristems

The term apical meristem refers to a group of meristematic cells at the apex of shoot and root which lay the foundation of the primary plant body by cell division.

At the shoot apex, the apical meristem denotes only the part of the shoot lying distal to the youngest leaf primordium, whereas the term shoot apex includes the apical meristem together with the subapical region bearing young leaf primordia (Cutter, 1965).

However, in roots, the small group of cells at the extreme apex, called the **quiescent center**, divide very infrequently and the highest rate of cell divisions is observed in adjacent tissues of the root tip. The planes of cell division in the root meristem are strictly ordered, and are primarily transverse divisions that provide growth of the root in length. As the result of such ordered divisions, characteristic cell tiers are formed.

Like other meristems, the apical meristems are also composed of initials, which perpetuate the meristems, and their derivatives. Also the derivatives usually divide and produce one or more generations of cells before the cytologic changes leading to differentiation of specific cells and tissues.

Evolution of the concept of apical organization

Apical Cell Theory

In cryptogams like algae, bryophytes and pteridophytes the solitary apical meristematic cell leads to the whole process of growth. Many early botanists believed that the same condition prevails in all higher plants. On that

assumption, the *Apical Cell Theory* was put forward by Hofmeister and supported by Nageli in 1878.

Subsequently, however, it was found that the complex apices of gymnosperms and angiosperms could not be interpreted by this apical theory. These plants do not have a solitary apical meristematic cell. They rather have a group of meristematic cells.

So, soon it became accepted that the apical cell theory is not applicable to seed plants.

Histogen Theory

The histogen theory was developed by Hanstein (1868, 1870) on the basis of extensive studies of angiosperm shoot apices and embryos.

According to this theory the main body of the plant arises not from superficial cells but from a massive meristem of considerable depth comprising three parts, which are known as the histogens. The histogens may be distinguished by their origin and course of development.

The outermost part, **the dermatogen**, is the precursor of the epidermis; the second, the **periblem**, gives rise to the cortex; the third, the **plerome**, constitutes the inner mass of the axis.

The dermatogen, each layer of the periblem, and the plerome begin with one or several initials distributed in superposed tiers in the most distal part of the apical meristem.

The Histogen type of apical meristem organization may be seen in many roots but rarely in shoots. Thus the subdivision into dermatogen, periblem, and plerome has no universal application. Further, a big flaw of Hanstein's histogen theory is its presumption that the destinies of the different regions of the plant body are determined by the discrete origin of these regions in the apical

meristem. In plants, the origin of different regions of the plant body from the sharply- defined histogens cannot be demonstrated.

Tunica-Corpus Theory

The *Tunica-Corpus Theory* of A. Schmidt (1924) was an outcome of observations on angiosperm shoot apices.

It states that the initial region of the apical meristem consists of

1. **The tunica**, one or more peripheral layers of cells that divide in planes perpendicular to the surface of the meristem (anticlinal divisions), and
2. **The corpus**, a body of cells several layers deep in which the cells divide in various planes. Thus, whereas the corpus adds bulk to the apical meristem by increase in volume, the one or more layers of tunica maintain their continuity over the enlarging mass by surface growth.

Each layer of tunica arises from a small group of separate initials, and the corpus has its own initials located beneath those of the tunica. In other words, the number of tiers of initials is equal to the number of tunica layers plus one, the tier of corpus initials.

Although the epidermis usually arises from the outermost layer of tunica, the underlying tissues may have their origin in the tunica or corpus or both, depending on the plant species and the number of tunica layers.

As more plants came to be examined, the tunica-corpus concept underwent some modifications, especially with regard to the strictness of the definition of the tunica. According to one view, tunica should include only those layers that never show any periclinal divisions in the median position, that is, above the level of origin of leaf primordia (Jentsch, 1957).

Mantle core concept

This concept was proposed by Popham and Chan in 1950. The term mantle is used for the dome-shaped outer layers of the apex, and the core for the inner cell mass covered by the mantle. In this concept mantle is used for tunica and the core for corpus.

The current concept of shoot apex in angiosperms

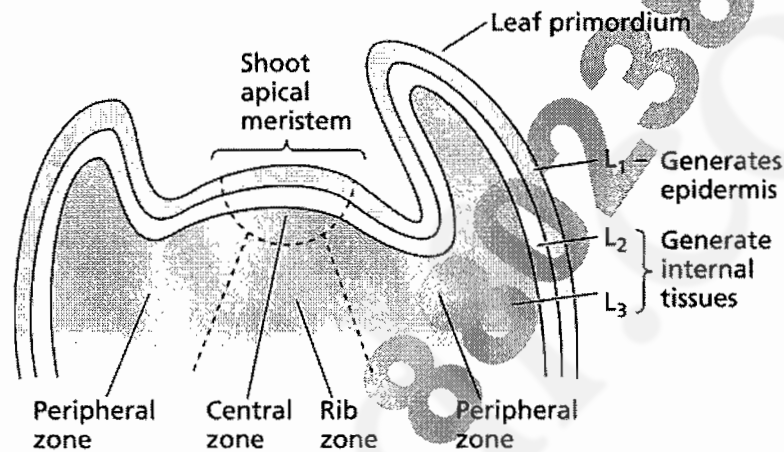


Figure: Angiosperm shoot apex organisation

The shoot apical meristem consists of different functional regions that can be distinguished by the orientation of the cell division planes and by cell size and activity.

The angiosperm vegetative shoot apical meristem usually has a highly stratified appearance, typically with *three distinct layers of cells*. These layers are designated L₁, L₂, and L₃, where L₁ is the outermost layer. Cell divisions are anticlinal in the L₁ and L₂ layers; that is, the new cell wall separating the daughter cells is oriented at right angles to the meristem surface. Cell divisions are less regularly oriented in the L₃ layer.

Active apical meristems also have an organizational pattern called cytohistological zonation. Each zone is composed of cells distinguished not only on the basis of their division planes, but also by differences in size and by

degrees of vacuolation. These zones exhibit different patterns of gene expression, reflecting the different functions of each zone.

The center of an active meristem contains a cluster of relatively large, highly vacuolate cells called the central zone. The central zone is somewhat comparable to the quiescent center of root meristems. A surrounding region of smaller cells is called the peripheral zone. A rib zone lies underneath the central cell zone and gives rise to the internal tissues of the stem.

These different zones most likely represent different developmental domains. The peripheral zone is the region in which the first cell divisions leading to the formation of leaf primordia will occur. The rib zone contributes cells that become the stem. The central zone contains the pool of stem cells, some fraction of which remains uncommitted, while others replenish the rib and peripheral zone populations (Bowman and Eshed 2000).

Root apex organization

From the root apical meristem different tissues of the root are formed. It has been observed that in certain Pteridophytes, like the members of Polypodiaceae, Ophioglossaceae and *Equisetum*, the entire root develops from a single tetrahedral apical cell, while in others, e.g. the Marattiaceae, the root is developed from a group of initials.

In seed plants there is a larger group of initials in the root apex.

In root apex, protoderm, meristem of the cortex and meristem of the vascular cylinder are recognisable. It thus shows histogen type organization.

The special initials of the root cap are termed **calyptragen**.

Recently it has been found that a group of cells at the root have a very low mitotic activity. They appear in the form of a hemisphere or a disc, termed the **quiescent centre**. The mitotically active cells lying over the surface of the

quiescent centre are regarded as temporary initials. *In vitro* culture of isolated quiescent centre shows that it has got the capacity to regenerate a new root independently.

There are many views as to why a quiescent centre appears in the root :

- Hormones may be synthesised in the quiescent centre and may stimulate division at low concentration and inhibit at high concentration.
- There is a competition between cells for supplies of nutrients or hormones.
- The root cap controls quiescence in the particular portion of the meristem.
- The pressure exerted by the rapidly dividing neighbouring cells causes the inactivity in the quiescent centre.

The Korper-Kappe Theory

The theory was put forward by Schuepp (1917). It is similar to the tunica-corpus theory of the shoot apex. It is based on differences in the planes of cell division. The theory says that the cells in the root apex divide in a pattern called T-divisions.

The outer region of the root apex is the **Kappe**. The cells of this region divide first horizontally. The lower daughter cell then divides longitudinally, i.e. at right angles to the plane of the first division. Thus the planes of the two divisions form a T in a median longitudinal section of the root.

The inner region of the apex is the **korper**. In this region the T is inverted, i.e. the second division takes place in the upper daughter cell. This type of division has been found among the members of Gramineae and Fagaceae.

Stomatal anatomy

Introduction to the stomata

What Are Stomata?

A stoma (*pl.* stomata) is a microscopic pore, found in the epidermis of the green and photosynthetic parts of higher plants and also in moss sporophytes. It is surrounded by a pair of specialized epidermal cells called guard cells, which act as a turgor-driven valve that open and close the pores in response to given environmental conditions. Their main function is to allow gases such as carbon dioxide, water vapours and oxygen to move rapidly into and out of the leaf. In green leaves they occur either on both surfaces (**amphistomatic** leaf) or on one only, either the upper (**epistomatic** leaf) or more commonly the lower i.e., **hypostomatic** leaf.

How are the Stomata Distributed?

In the Plant World

1. All the Pteridophytes, Gymnosperms and Angiosperms on most of the green pigmented aerial structures; leaves, floral leaves, green stem epidermis etc. Submerged aquatics are exception.
2. Among Bryophytes, only the sporogonium bears functional stomata and that too in two groups – Mosses and Hornworts.

On an Angiosperm Leaf

The major patterns are:

1. Submerged aquatics: No stomata on the leaves
2. Aquatics with exposed leaves: Stomata on the exposed surface; e.g. on the upper surface of the leaf in *Lilium*

3. Terrestrial monocots: Stomata on both the sides, almost equal density ($50 - 200 / \text{mm}^2$), e.g. *Allium*, *Hordeum*, *Triticum*, *Maize*
4. Herbaceous dicots: Stomata on both the sides, but greater density on the lower surface of the leaves ($30 - 120 / \text{mm}^2$ on the upper surface, while $150 - 250 / \text{mm}^2$ on the lower surface). e.g. *Nicotiana*, *Medicago*, *Pelargonium*
5. Woody species: Stomata almost exclusively on the lower surface of the leaf ($200 - 800 / \text{mm}^2$) seen in *Quercus*, *Tilia*

Structure of the stomata

A. deCandolle (1827) first called the epidermal pores as stoma, which in Greek means mouth. The **pores** (also known as **apertures**) are the intercellular space between the two **guard cells**, which together with the pore constitute the **stoma** (plural: stomata). In many plants, some epidermal cells are associated with the guard cells. These are **subsidiary cells**. (Fig. 1)

The term **stomatal complex** or **apparatus** refers to the guard cells and subsidiary cells collectively. Below each stoma, there is large intercellular space, directed inwards to the mesophyll, called **sub-stomatal chamber**.

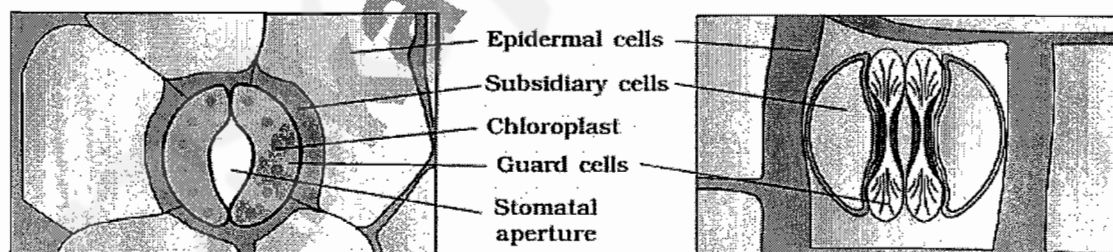


Figure 1: Diagrammatic representation: (a) stomata with bean-shaped guard cells (b) stomata with dumb-bell shaped guard cell

Subsidiary cell: These are specialized epidermal cells and differ in shape, size and cell content from the guard cells and the epidermal cells. They are also called **accessory cells** and lie in close proximity or adjacent to guard cells. In

Equisetum the subsidiary cells overarch the guard cells. Subsidiary cells are generally smaller than the normal epidermal cells and in contrast to epidermal cells they contain dense cytoplasm and greater frequency of cell organelles. Generally chloroplasts and anthocyanins are absent in subsidiary cells. In some grasses, they take part in the mechanism of opening and closing of stomata. In grasses no plasmodesmata or pit were observed between the subsidiary cells and guard cells, but they exist in the leaves of *Vicia faba* and *Nicotiana*.

Guard cell: It is a specialized epidermal cell that differs in shape, size and cell content from the normal epidermal cells and subsidiary cells. A pair of guard cell and the intercellular space, termed pore, present between them constitute a stoma. There is report that the stoma of *Azolla pinnata* (Sen, 1983) consists of unicelled and binucleate guard cell with a pore, and the stoma is associated with one or more subsidiary cells on its proximal side. Two basic forms of guard cells are observed (Fig. 1):

1. *Reniform or kidney or crescent-shaped guard cells:* A pair of such cell is attached to each other by their concave ends to form a stoma that appears elliptical in surface view, Eg. Dicotyledons.
2. *Dumb-bell shaped guard cells:* Eg. Gramineae, some members of Cyperaceae, Palmae, Marantaceae etc. The bulbous ends of guard cells are connected to each other by a narrow middle section.

Functional Anatomy of the Guard Cells

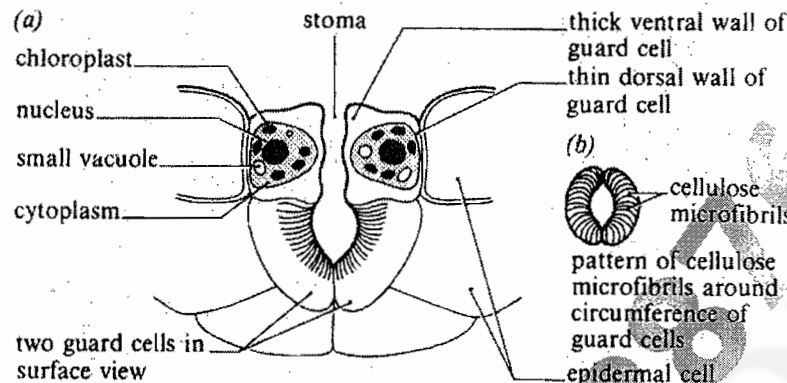


Figure 2: Fine structure of the guard cells, showing radial micellation.

Investigations on sub-microscopic anatomy of guard cell walls suggest that the special orientation of cellulose micro fibrils and micelles are mainly responsible for opening and closing of stomatal pores (Krikorian et. al., 1973). These studies have shown that cellulose micro fibrils and micelles are arranged around the circumference of the elongated guard cells (Fig. 2). A greater density of radiating micro fibrils on the ventral walls makes them less flexible. This arrangement is called **radial micellation**. Such guard cells, when take up water and expand, cannot increase much in diameter because the micro fibrils on the ventral walls do not stretch much. On the other hand, they increase in length. Since the two guard cells remain attached to each other at both ends, they bend outward on swelling and result opening of stomatal pore.

Origin of stoma

The protoderm cell, known as **stomatal meristemoid**, by several divisions gives rise to a stoma. This cell is usually isodiametric or polygonal in shape and possesses a single conspicuous nucleus with denser cytoplasm. The term **guard cell initial** or **guard cell mother cell** (GCMC or gcmc) denotes a cell whose bisection forms the sister guard cells of a stoma (Pant, 1965).

Usually the stomatal meristemoids are initiated between the mature stomata (e.g., gymnosperms and angiosperms). Sometimes their origin is acropetal (e.g., stem of *Psilotum*); basipetal origin is observed in Lycopodiales, Convolvulaceae, Rubiaceae etc. while simultaneous differentiation are observed in *Erythrina*, a member of Leguminosae. The differentiation of a stomatal meristemoid and its subsequent divisions leading to the formation of a stoma varies from group of plants.

In *Allium cepa* the stomatal meristemoid is an elongated protoderm cell. Its ontological fate is shown in Figure 3.

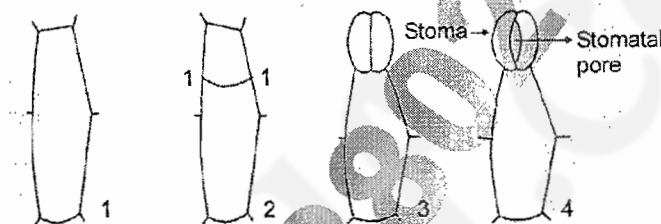


Figure 3: The origin of stoma in *Allium*. 1. The stomatal meristemoid cell 2. A transverse division in the stomatal meristemoid forms the GCMC 3. A longitudinal division in the GCMC forms a pair of Guard Cells 4. The intercellular space between the guard cells is the stomatal pore.

An unequal division of this cell forms a large cell and a small cell that is rich in protoplasm. The small cell is the gcmc whose longitudinal bisection forms the future two sister guard cells. At the time of formation, the guard cells are small, remain pressed with each other and have no definite shape. As they mature, the middle lamella present between the two sister guard cells swell and they become lens shaped. As a result the connection between the guard cells weakens. Then enzymatic dissolution of the bulged portion of middle lamella occurs where the pore of the stoma is formed. Each guard cell secretes pectinase, which break down the pectinaceous middle lamella. The two guard cells gradually separate from each other at the pore region and become reniform. The osmotic force developed in the guard cells due to starch hydrolysis helps to assume the

characteristic shape. The stoma of *Allium* lacks subsidiary cells. A single stomatal meristemoid gives rise to the stoma.

The stomatal complex of many genera contains variable number of subsidiary cells whose origin differs and accordingly the following three ontogenetic types of stoma are recognized (Pant, 1965) [Fig. 4].

1. **Mesogenous** : When the subsidiary cells and guard cells of a stomatal complex are derived from a single stomatal meristemoid, the stoma is said to be mesogene and its development is termed as mesogenous type. According to the number of subsidiary cells the stomatal meristemoid may have four cutting faces (e.g., *Lactuca viscosa*), three anticlinal cutting faces (e.g., *Beta vulgaris*, *Datura stramonium*, *Nicotiana* etc.), two parallel cutting faces (e.g., *Rubiaceae*, *Casuarina*, *Gnetum gnemon*, *Ricinus communis* etc.).
2. **Perigenous** : When all the subsidiary cells of a stomatal complex are derived from protodermal cell that is independent of the guard cell mother cell, the stoma is designated as perigene and its development is termed as perigenous type. The initials of the subsidiary cells lie adjacent to guard cell mother cell. These neighbouring cells directly or their derivatives form the subsidiary cells. The guard cell mother cell divides only once and the two cells, thus produced, form the two guard cells. Ex. *Lycopodium*, *Ephedra*, *Trapa*, *Cuscuta* etc.

Types of stoma	Meristemoid	First division	Second division	Third division	Mature stoma
Mesogenous					
Perigenous					
Mesoperigenous					

Figure 4: Origin types of stomata

3. **Mesoperigenous** : In this developmental type the subsidiary cells are of dual origin. In the stomatal complex the guard cell mother cell and one subsidiary cell are formed from a single stomatal meristemoid; the other subsidiary cells are derived from the neighbouring cells, which are adjacent to guard cell mother cell. The first division of the stomatal meristemoid and the partition of the guard cell mother cell to form two guard cells may be:

- parallel (e.g., *Tetracentron sinensis*) or
- at right angles (eg. Some members of *Onagraceae* and *Caryophyllaceae*) or
- at other angles (e.g., *Ranunculus*) to each other.

Florin (1933) had earlier described two stomatal patterns in gymnosperm that was termed:

1. **Haplocheilic stoma**: In this type the protoderm cell or stomatal meristemoid functions directly as guard cell mother cell (gcmc) without any prior division at all. The gcmc gives rise the guard cells of the stoma. The subsidiary cells are formed from the neighbouring specialized protoderm cells. Such subsidiary cells, whose mother cells are distinct from gcmc and not

derived from the stomatal meristemoid, are termed as perigene. Ex. Cycadales, Pteridospermopsida, Coniferopsida, *Ephedra* etc.

2. **Syndetocheilic stoma:** In this type, the protoderm cell or stomatal meristemoid divides and the resulting cells are differentiating into GCMC and the initials of subsidiary cells. Such subsidiary cells thus derived from the stomatal meristemoid that also produces gmc are termed as mesogene. Ex. Cycadeoidales, *Gnetum*, *Welwitschia* etc.

The perigenous and mesogenous stomatal complexes (Pant, 1965) are ontogenetically similar to Florin's haplocheilic and syndetocheilic type respectively.

Later studies on stomatal ontogeny refuted the concept of perigenous stoma where the protoderm cell functions directly as gmc.

Payne (1979) proposed a basic classification scheme of stomatal complex based on the mode of division of guard mother cell (GCMC) with respect to the wall that formed the GCMC. The GCMC divides to form a pair of guard cell. The orientation of the wall that separates the guard cells may be perpendicular, parallel or have no special orientation with respect to wall that cuts the GMC from stomatal meristemoid (Fig. 5). Accordingly the following three types are recognized:

1. **Diameristic** (Dia = across and meros = part or portion) : In this type the stomatal meristemoid cuts off the GCMC at the distal end. The GCMC divides and the division wall is perpendicular to the wall that formed the GCMC. Thus, the stoma is formed at right angles to the wall that formed the GCMC. The subsidiary cells may be mesogene (e.g., Lamiaceae) or mesoperigene (e.g., monocot, Caryophyllaceae).
2. **Parameristic** (Para = beside and meros = part or portion) : In this type the stomatal meristemoid cuts off the GCMC. The division of GCMC is by a wall, which is parallel to the preceding division wall. Thus, the stoma is

formed parallel to the wall that cuts the GCMC. The subsidiary cells may be mesogene (Ex. Cruciferae, Rubiaceae) or mesoperigene (*Liriodendron*).

3. **Anomomeristic** (Anomalos and meros = part or portion): In this type, the stomatal meristemoid cuts off the GCMC. The division of the GCMC is by a wall that has no special orientation to the previous wall. The division may be at any angle with respect to the preceding wall and thus the stoma lies at any angle to the wall that forms the GCMC. The subsidiary cell is usually single and mesogene. Ex. *Ranunculus*.

The substomatal cavity present below each stomatal complex is formed by the natural extension of existing air spaces and dissolution of some of the mesophyll cells.

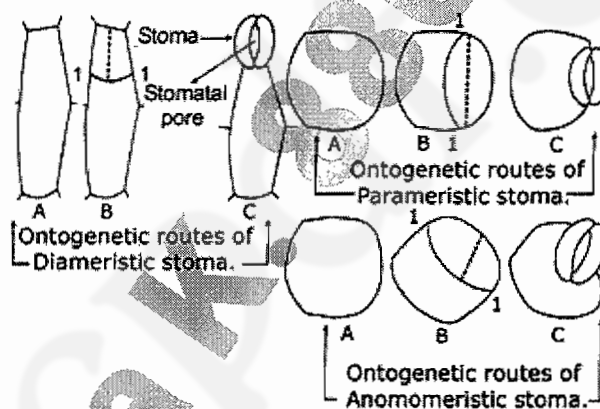


Figure 5: A basic classification scheme of stomatal complex based on the mode of division of guard mother cell (GCMC) with respect to the wall that formed the GCMC.

Types of stoma

Based on arrangement of the epidermal cell neighbouring the guard cell, more than 25 main types of stomata in dicots have been recognized (Metcalf & Chalk, 1979). Besides this, there are various reports available on further types of stomatal complexes of dicots.

The following types of stoma are commonly noted in anatomical descriptions (Fig. 6). The description of the stomatal complexes is based on light microscopy only.

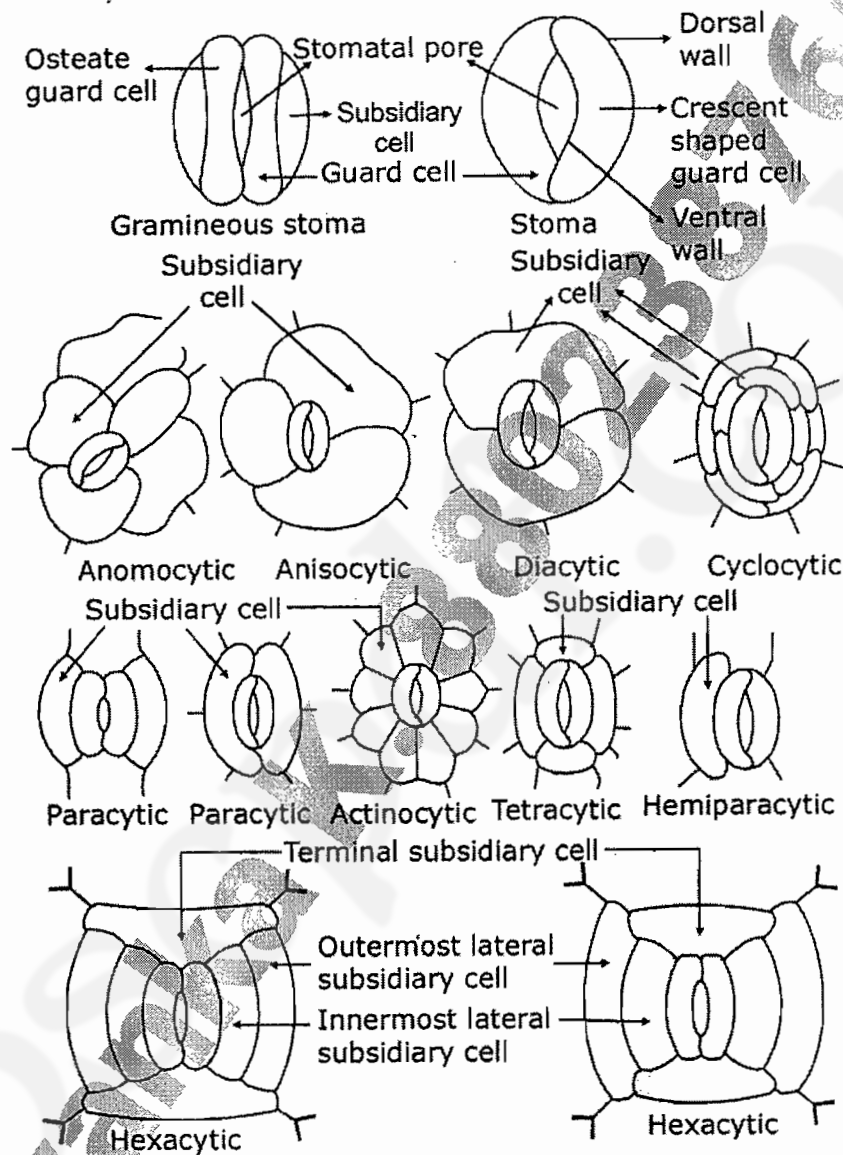


Figure 6: Different types of stomata

1. **Anomocytic** (irregular-celled / Ranunculaceous) type: The subsidiary cells surrounding the stoma are indistinguishable in size and form from the neighbouring epidermal cells. The number and arrangement of subsidiary

cells may not be definite. The guard cells appear to be embedded in ordinary epidermal cells. Ex. *Cucurbita*, *Capparidaceae*, *Malvaceae*, *Papaveraceae* etc.

2. **Anisocytic** (unequal-celled / Cruciferous) type: The stoma is surrounded by three subsidiary cells of which one is distinctly smaller or larger in size than the other two. The subsidiary cells may not be very distinct from ordinary epidermal cells. Ex. *Petunia*, *Solanum*, *Sedum*, *Nicotiana* etc.
3. **Paracytic** (parallel-celled / Rubiaceous) type: The stoma is accompanied by two or more (usually two) subsidiary cells that lie parallel to the long axis of guard cells and pore. Ex. *Phaseolus*, *Arachis*, *Psoralea* etc.
4. **Hemiparacytic** type: The stoma is accompanied by a single subsidiary cell, which is placed parallel to the long axis of the pore and this cell may be long or short in length in contrast to the guard cells. Ex. *Tetracentron*.
5. **Diacytic** (cross-walled / Labiatous or Caryophyllaceous) type: The stoma is enclosed by two large subsidiary cells whose common wall is aligned perpendicular to the long axis of the pore and guard cells. Ex. *Hygrophila*, *Dianthus* etc.
6. **Actinocytic** type: The stoma is surrounded by four or more subsidiary cells, which are radially elongated and aligned radially around the stoma. -Ex. *Ancistrocladus*.
7. **Cyclocytic** type: The stoma is surrounded by four or more subsidiary cells, which form a narrow ring around the guard cells. Ex. *Lumnitzera*, *Laguncularia* etc.
8. **Tretracytic** type: This type includes four subsidiary cells among which situated on the polar side and the other two on the lateral side of guard cells. Ex. *Rhoeo*.
9. **Hexacytic** type: The stoma is surrounded by six subsidiary cells among which two are situated on the two polar sides and rest two pairs occur on the

two lateral sides being parallel to the long axis of the guard cells. The size of subsidiary cells may be of two different types: (a) the two polar cells may be as broad as stomatal complex (e.g., *Geogenanthus*) and (b) the length of the outer most subsubsidiary cells may be as long as stomatal complex (e.g., *Commelina*).

10. Gramineous type: Metcalfe and Chalk (1950) described this type of this type is confined to monocotyledons and it is characteristic of the Gramineae and Cyperaceae. The guard cell is dumb-bell-shaped or osteate. The two ends of the guard cell are bulbous and the middle portion is much narrower and straight. In the narrow portion, the cell wall is strongly thickened. The bulbous part is relatively thin walled. The two dumb-bell-shaped guard cells are attached to each other by their bulbous ends thus forming a slit like pore. The subsidiary cells occur parallel to the long axis of the pore.

Stebbins and Khush (1961) reported four types of stomatal complex in monocotyledons for which they did not introduce any verbal terminology and distinguished the pattern groups only as first, second, third and fourth type, which are as follows (Fig. 7).

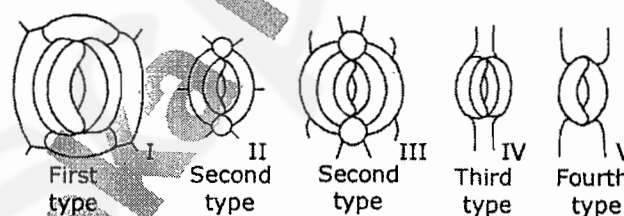


Figure 7: The various types of stomata in Monocotyledons

1. **First type:** The two guard cells of a stoma are surrounded by four to six subsidiary cells in all four directions, i.e., two polar and two lateral sides. The stoma of *Tradescantia*, *Rhoeo* and *Zebrina* are surrounded by four subsidiary cells each of which are present on the four sides of paired guard cells; thus the stoma appears as a square on surface view. The stoma of *Commelina* has six

subsidiary cells of which four are situated on the two lateral sides and the rest at the ends of guard cells.

2. **Second type:** The two guard cells of a stoma are surrounded by four to six subsidiary cells of which two are smaller and more or less round than the rest and each lies at the poles of the guard cells; the rests are arranged lateral to the guard cells. Ex. *Pandanus haerbachii*, members of Palmae and Cyclanthaceae. In Palmae there are variations: the genera *Caryota* and *Calamus* have two subsidiary cells only on the two lateral sides of a stoma in contrast to *Phytelephas* where the stomatal complex is with distinct six subsidiary cells.
3. **Third type:** The two guard cells of a stoma are surrounded by two subsidiary cells each of which lie on the lateral sides of guard cells. Ex. *Juncus effusus*. This is the most common and predominant type of stomatal complex and spreads over 24 monocot families so far investigated. Ex. Gramineae, Cyperaceae, Juncaginaceae, Typhaceae, Liliaceae etc.
4. **Fourth type:** The pair of guard cells of a stoma is without any subsidiary cells. This is the second common type of stomatal complex and is found in the families Amaryllidaceae, Iridaceae, Orchidaceae, and Agavaceae etc.

Functional significance of different stomatal types

About 99% carbon dioxide used in photosynthesis is absorbed through stomata (lenticels and cuticles also absorb carbon dioxide to lesser extent). Earlier studies had confirmed that the more the subsidiary cells surrounding the guard cells, the faster the opening of the stoma (i.e. pore between the two guard cells) and vice versa.

In relation with this, plants that possessed stomata with many subsidiary cells (e.g. tetracytic and anomocytic types) will play important role in reducing greenhouse gases especially carbondioxide.

More over the other aspect of stomatal opening that favour water loss to the atmosphere (i.e. encouraging high rate of transpiration) is also advantageous by humidifying the atmospheric air.

Trichomes

Introduction to trichomes & their various types

Trichomes (a word of *Greek* origin, meaning a growth of hair) are epidermal appendages of diverse form, structure, and functions in higher plants. Trichomes are usually distinguished from the so-called emergences on the basis that the emergences are formed from both epidermal and sub-epidermal tissues, whereas **Trichomes are strictly epidermal appendages.**

According to Katherine Esau (1965) and Ray Evert (2008), trichomes are represented by:

1. Protective hairs
2. Supporting hairs
3. Glandular hairs
4. Scales
5. Various papillae
6. Absorbing hairs of the roots.

Occurrence

Trichomes may occur on all parts of a plant. Either they persist throughout the life of an organ, or they are ephemeral. Some persisting hairs remain alive; others become devoid of protoplasts and are retained in dry state. The epidermal trichomes usually develop early in relation to the growth of the organ.

Morphological Categories

Some morphological trichome categories are

1. **papillae**, which are small epidermal outgrowths often considered distinct from trichomes
2. **simple (unbranched) trichomes**, a large grouping of extremely common unicellular and multicellular trichomes
3. **two- to five-armed trichomes** of various shapes
4. **stellate trichomes**, all of which are star-shaped although variable in structure
5. **scales (peltate) trichomes**, consisting of a discoid plate of cells often borne on a stalk or attached directly to the foot
6. **dendritic (branched) trichomes**, which branch along an extended axis
7. **root hairs**
8. In addition there are many **specialized types of trichomes** such as stinging hairs, pearl glands, cystolith-containing hairs and water vesicles

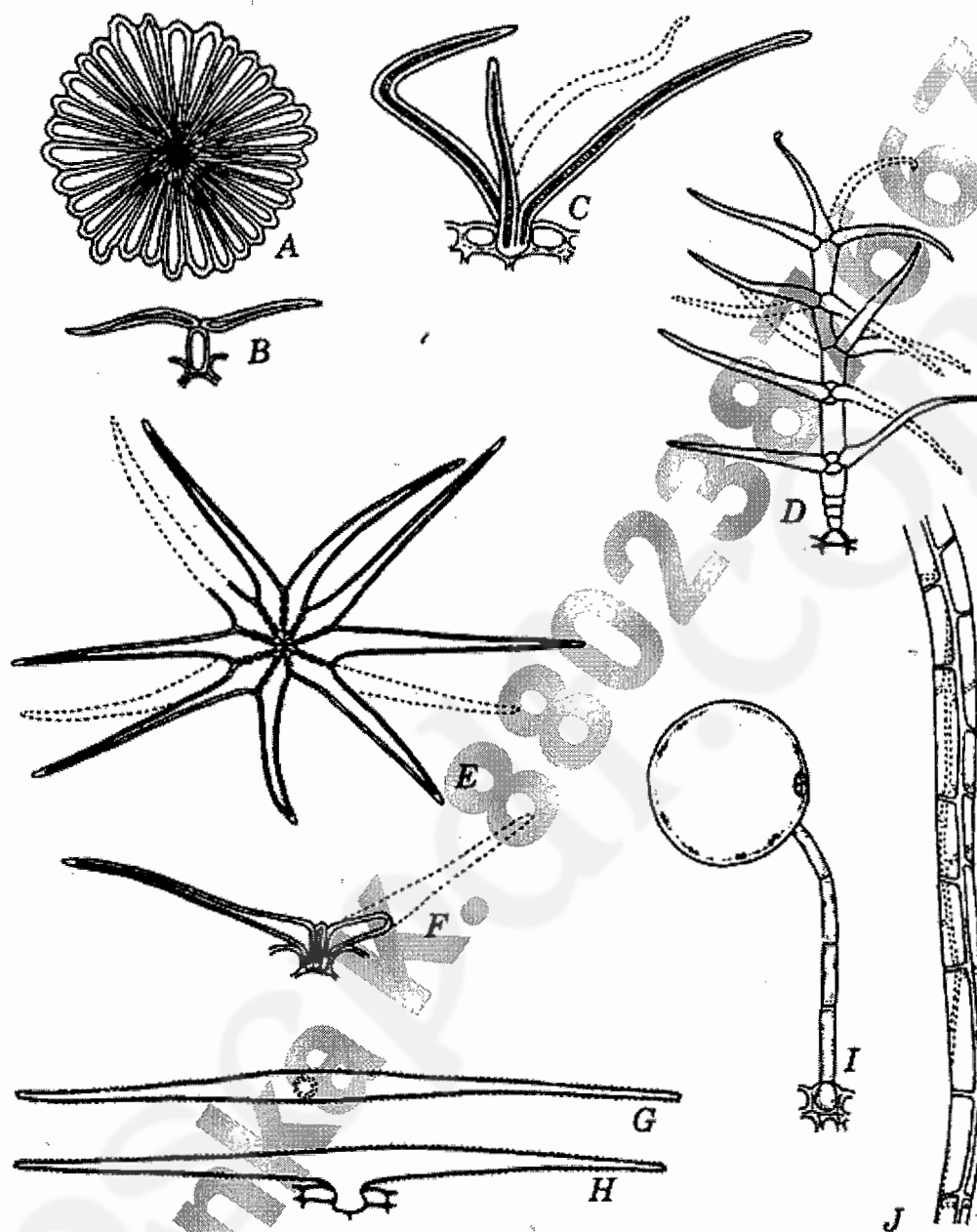


Figure 8: Various types of trichomes: A, B, peltate scale of *Olea* in surface (A) and side (B) views. C, tufted hair of *Quercus*. D, branched hair of *Platanus*. E, F, stellate hair of *Sida* in surface (E) and side (F) views. G, H, two-armed, T-shaped unicellular hair of *Lobularia* in surface (G) and side (H) views. I, vesiculate hair of *Chenopodium*. J, part of multicellular shaggy hair of *Portulaca*.

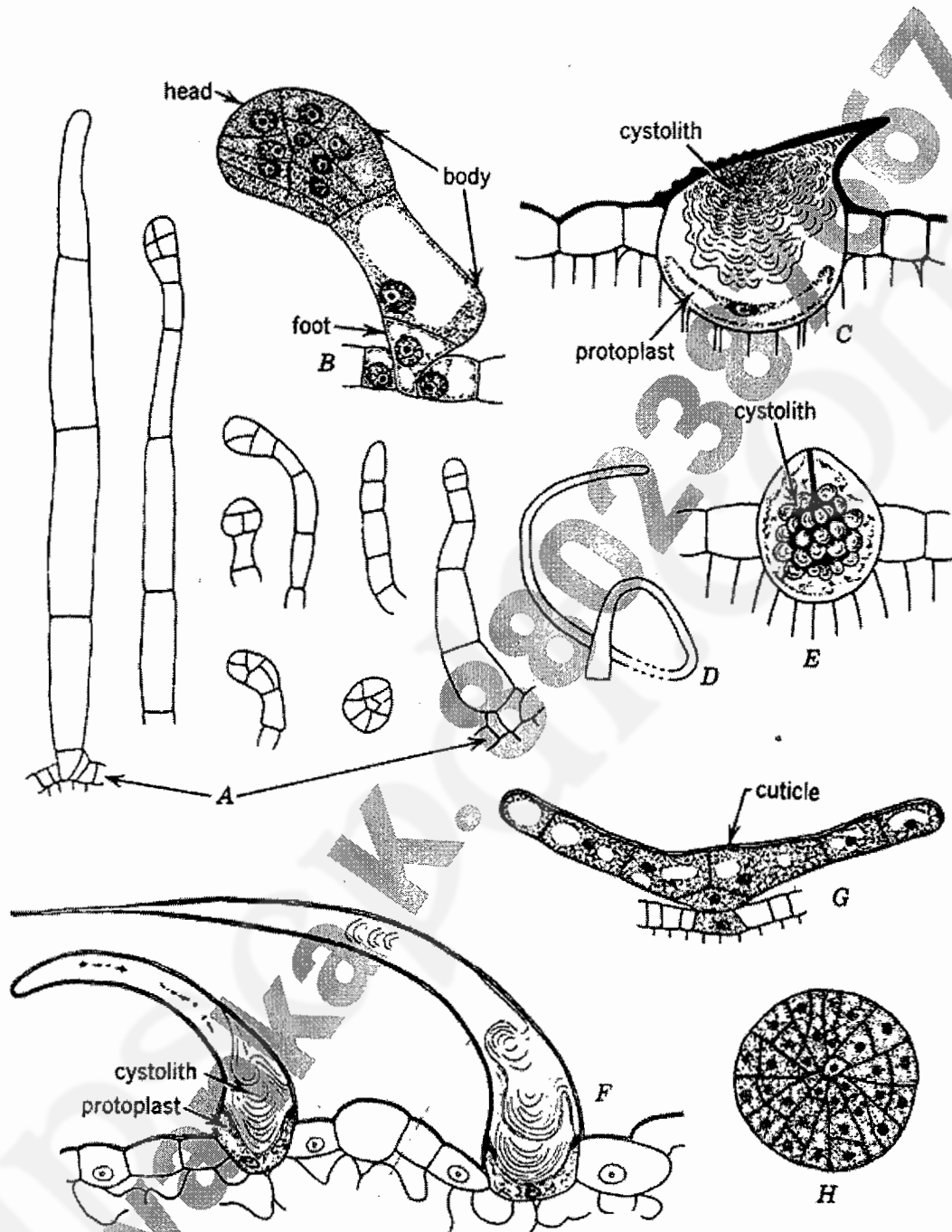


Figure 9: Trichomes in various forms: A, group of ordinary and glandular (with multicellular heads) hairs of *Nicotiana* (tobacco). B, enlarged view of glandular hair of tobacco, C, hooked hair with cystolith of *Humulus*. D, long coiled unicellular hair, and E, short bristle with cystolith of *Boehmeria*. F, hooked hairs with cystoliths of *Cannabis*. G, H, glandular peltate trichome of *Humulus* seen in sectional (G) and surface (H) views.

Glandular trichomes

Glandular trichomes contain volatile oils and other secretions that are produced by the plants. Unicellular, multicellular, and peltate hairs may be glandular. Some of the simple multicellular glandular hairs consist of a stalk and a unicellular or multicellular head. The head is also called the *Capitate Part* and it constitutes the secretory part of the hair. In a peltate glandular trichome the discoid plate is composed of glandular cells. Some glandular trichomes consist of a multicellular core of cells covered with a palisade like layer of secretory cells.

Often there is a variety of glandular trichome within the same taxon. In the Lamiaceae (Mint Family), there are two types of trichomes commonly found on leaves and stems: peltate and capitate. In 1999, L. Ascensão, L Mota and co-workers investigated the types of glandular trichomes and their distribution on leaves and flowers of *Plectranthus ornatus*. They reported five morphological types of glandular trichomes.

1. Peltate trichomes, confined to the leaf abaxial surface
2. Capitate trichomes, uniformly distributed on both leaf surfaces, are divided into two types according to their structure and secretory processes - long-stalked capitate trichomes, storing a heterogeneous secretion (a gumresin) and the short-stalked capitate trichomes, containing mainly polysaccharides.
3. Digitiform trichomes, on the leaves, which do not show a clear distinction between the apical glandular cell and the subsidiary cells, occur with a similar distribution to the capitate trichomes.
4. Conoidal trichomes located on the reproductive organs, particularly the calyx and corolla, exhibit long unicellular conical heads. A large apical pore, formed by tip disruption, releases the secretion (a gumresin)

5. Peltate trichomes which are numerous on the stamens and carpels – where digitiform, capitate and conoidal trichomes are absent.

Glandular trichomes contain or secrete a mixture of chemicals that have been found to have an enormous array of uses in the pesticide, pharmaceutical, and flavour / fragrance industries. Besides these industrial uses, glandular trichomes on some crop species confer resistance against insect pests. Thus, there is today an increasing interest in understanding the chemistry of glandular trichome exudates and taking advantage of their potential uses. For example, Glandular trichomes in *Mentha piperita* (peppermint) secrete I-menthone, which is converted to I-menthol, and the watersoluble neomenthol-glucoside, which is transported out of the gland. The possibility of manipulating the biosynthesis of Imenthol using recombinant DNA technology may be a boon to industries using menthol, such as cigarettes, liqueurs, perfumes, confectionery, cough drops and nasal inhalers.

Development of trichomes

All trichomes develop very early in the life of the organ. The unicellular cotton (*Gossypium*) trichome, commonly known as a cotton fiber, is initiated as a protuberance from a protodermal cell of the outer integument of the ovule. Development occurs synchronously for most of the trichomes, and their development can be divided into four somewhat overlapping phases.

Phase 1, fiber initiation occurs at anthesis as the fiber initials appear as distinct protuberances on the surface of the ovule.

Phase 2, fiber elongation begins soon afterward and continues for 12 to 16 days after anthesis. Whereas the microtubules are randomly oriented in the fiber initials, they become oriented transversely to the long axis of the cell as the fiber begins to elongate. The fibers undergo dramatic elongation, reaching lengths 1000 to 3000 times greater than their diameters.

Phase 3, secondary wall formation begins as the fiber approaches its final length and may continue for a further 20 to 30 days.

Phase 4, the maturation phase follows wall thickening. The fibers die, presumably by a process of programmed cell death, and become desiccated.

Molecular Genetic Control of Trichome Development: Molecular genetic control of trichome development has been studied in some detail in *Arabidopsis* in the recent years. The genes responsible for hairy trichome development are *GLABROUS1 (GL1)* and *TRANSPARENT TESTA GLABRA (TTG)*. They code for transcription factors and are essential for the initiation of trichome development.

Functions of trichomes

Trichomes have a variety of functions.

1. Plants growing in arid habitats tend to have hairier leaves than similar plants from more mesic habitats. Studies of arid-land plants indicate that increase in leaf pubescence (hairiness) reduces the transpiration rate by increasing the reflection of solar radiation, which lowers leaf temperatures, and increasing the boundary layer (the layer of still air through which water vapor must diffuse).
2. The basal or stalk cells of the trichomes of at least some xeromorphic leaves are completely cutinized, preventing apoplastic water flow into the trichomes.
3. Many “air plants” such as epiphytic bromeliads utilize foliar trichomes for the absorption of water and minerals.
4. In the saltbush (*Atriplex*), salt-secreting trichomes remove salts from the leaf tissue, preventing an accumulation of toxic salts in the plant.

5. During the early stages of leaf development polyphenol-containing trichomes may play a protective role against UV-B radiation damage.
6. Trichomes may provide a defense against insects. In numerous species, trichome density is negatively correlated with insect responses in feeding and oviposition and with nutrition of larvae. Hooked trichomes impale insects and their larvae. Secretory (glandular) trichomes may provide a chemical defense whereas some insect pests are poisoned by trichome secretions, others are rendered harmless by immobilization in the secretion.

C4 leaf (Kranz type) Anatomy

The essentials of C4 leaf (Kranz type) Anatomy

Kranz anatomy refers to a specific type of leaf anatomy, seen in *most but not all* plants with C4 photosynthetic metabolism.

Definition: It is a leaf anatomy in which the mesophyll cells form compact concentric rings around the bundle sheath of the leaf, giving a wreath like appearance and there is dimorphism in chloroplasts of bundle sheath and mesophyll cells.

It was first reported by G. Haberlandt in 1901 as **Kranz Syndrome**.

It is an adaptation for minimizing the photorespiratory process and facilitate C4 metabolism, especially in plants of tropical origin. The essence of this process, which was elucidated by **M. D. Hatch and C. R. Slack**, is that *four-carbon (C₄) compounds such as oxaloacetate and malate carry CO₂ from mesophyll cells, which are in contact with air, to bundle-sheath cells, which are the major sites of Calvin Cycle.*

About 8000 species of angiosperms, in 19 different families, have Kranz Anatomy. The most important of the C4 metabolising families include Poaceae, Aizoaceae, Amaranthaceae, Compositae, Chenopodiaceae, Cyperaceae, Euphorbiaceae, , Nyctaginaceae, Portulacaceae, and Zygophyllaceae. C4 carbon fixation is less common in dicots than in monocots, with only 4.5% of dicots using the C4 pathway, compared to 40% of monocots. Despite this, only three families of monocots utilise C4 carbon fixation compared to 15 dicot families. Of the monocot clades containing C4 plants, the grass (Poaceae) species use the C4 photosynthetic pathway most. Forty-six percent of grasses are C4 and together account for 61% of C4 species. These include the food crops maize, sugar cane, millet, and sorghum.

The construction of a C4 leaf

Most but not all plants with C4 metabolism possess a specialized leaf anatomy called **Kranz Anatomy**.

Kranz, the German word for "halo," or "wreath," refers to a ring of mesophyll cells just to the outside of another ring of large bundle-sheath cells, both of which encircle the vascular bundle.

In transverse sections viewed under the microscope, the two cell layers give the appearance of a wreath surrounding each bundle. The rings make the Bundle Sheath, contain starch-rich chloroplasts lacking grana which differ from those in mesophyll cells present as the outer ring.

Hence, the chloroplasts are called dimorphic. This peculiar anatomy is called Kranz Anatomy.

In addition to the unique "wreaths," other features that typify leaves with Kranz anatomy include small intercellular spaces, and frequent veins.

In comparison to a C3 leaf, there is considerable anatomic variation in the arrangement of the bundle sheath cells and the mesophyll cells in a C4 leaf.

- a. The vascular bundle is surrounded immediately outside by the bundle sheath ring.
- b. The bundle sheath cells have larger chloroplasts with large amounts of starch but no granal system. The thylakoid system is organized as *peripheral reticulum*.
- c. The bundle sheath ring is surrounded by one or more compact rings of mesophyll cells.
- d. The mesophyll cells have normal granal system but no RuBisCO activity.

- e. An extensive network of plasmodesmata connects mesophyll and bundle sheath cells.

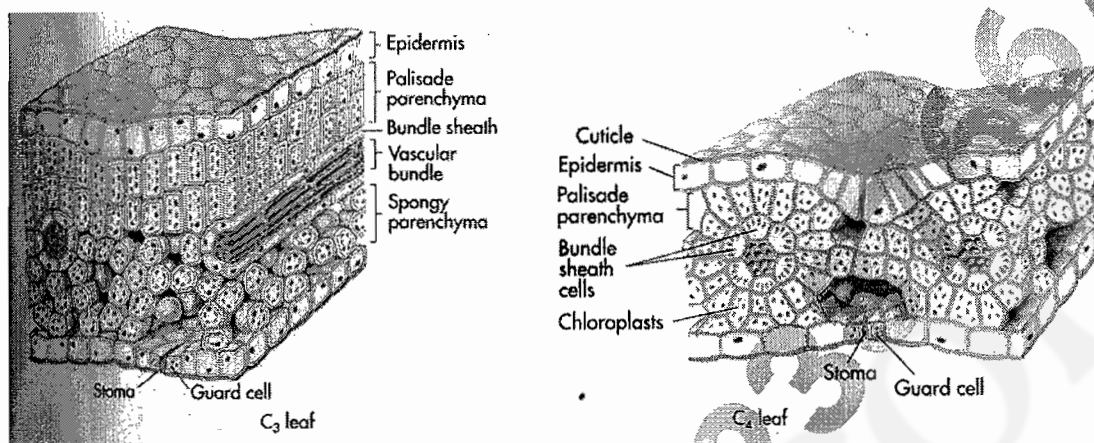


Figure: C3 and C4 leaf anatomies

Functional importance of Kranz Anatomy

Kranz anatomy is an adaptation for CO_2 concentration and minimizing the photorespiratory process.

There is a division of labour between two kinds of photosynthetic cells of C4 plants, mesophyll cells and bundle sheath cells (Campbell and Black, 1982). Malate and aspartate are formed in mesophyll cells, and 3-PGA, sucrose and starch are produced mainly in bundle sheath cells. RUBISCO exists only in bundle sheath cells, so the complete Calvin cycle (C3 cycle) occurs only in bundle sheath cells. On the other hand, PEP carboxylase occurs mainly in mesophyll cells performing C4 cycle.

The primary function of the Kranz is to provide a site in which CO_2 can be concentrated around RUBISCO, thus reducing photorespiration. In order to facilitate the maintenance of a significantly higher CO_2 concentration in the bundle sheath cells compared to those of mesophyll, the boundary layer of Kranz has a low conductance to CO_2 , a property which may be enhanced by the presence of suberin.

Kranz anatomy is an adaptation for CO_2 plants living in tropics.

Such plants initially fix CO_2 in mesophyll cells as

4-C compounds, and later releases CO_2 in bundle sheath cells. Though there is an additional ATP requirement (2ATP) for each molecule of CO_2 utilized in this pathway.

There is better utilization of available water by reducing the intensity of solar radiation by closely packed mesophyll cells. Due to presence of organic acids in mesophyll cells, C_4 plants can tolerate high salinity. Such plants can maintain high photosynthetic rates under low CO_2 concentration when stomata are nearly closed. Thus C_4 plants have a comparative advantage over C_3 plants under conditions of drought, high temperatures and nitrogen and CO_2 limitations.

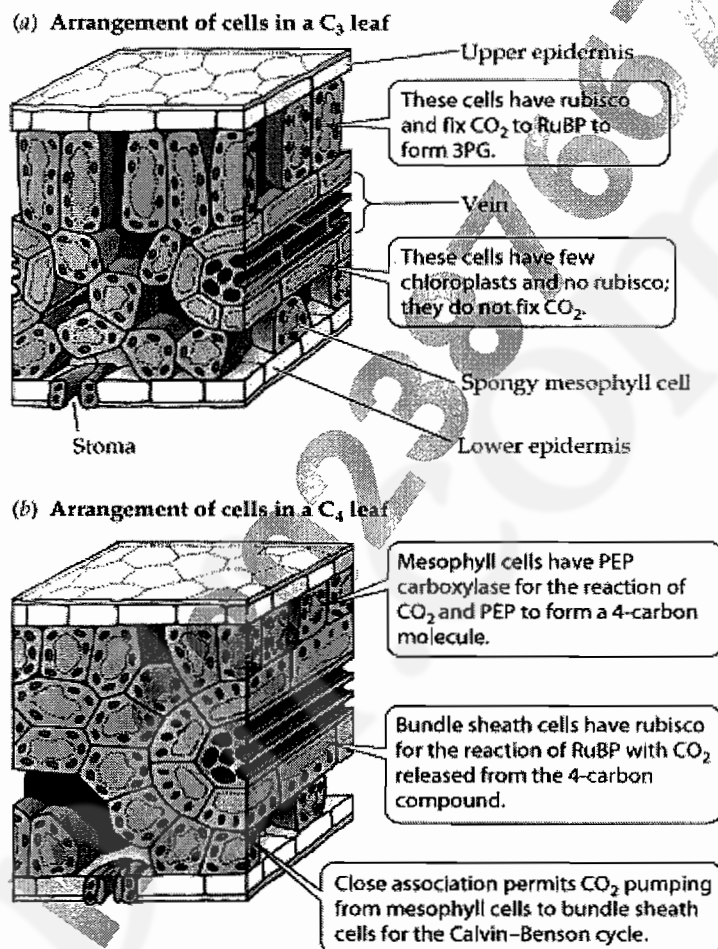


Figure: Functional importance of Kranz Anatomy

Is Kranz Anatomy Universal in C₄ Plants?

Recent evidences point out that the Kranz Anatomy is common in the C₄ plants but not universal.

1. On 26 October 2000, **Nature** reported the discovery of both the C₃ and C₄ pathways in a marine diatom *Thalassiosira*. In this unicellular organism, the two paths are kept separate by having the C₄ path in the cytosol, and the C₃ path confined to the chloroplast. The presence of a C₄ pathway probably reflects the frequent low concentrations of CO₂ in ocean waters.
2. A report in the 24 January 2002 issue of **Nature** (by Julian M. Hibbard and W. Paul Quick) describes the discovery that **tobacco**, a C₃ plant, has cells capable of fixing carbon dioxide by the C₄ path. These cells are clustered around the veins (containing xylem and phloem) of the stems and also in the petioles of the leaves. In this location, they are far removed from the stomata that could provide atmospheric CO₂. Instead, they get their CO₂ and/or the 4-carbon malic acid in the sap that has been brought up in the xylem from the roots.
3. In 2003, Voznesenskaya, Elena V and co-workers showed that C₄ photosynthesis can function within a single photosynthetic cell in terrestrial plants. *Borszczowia aralocaspica* and *Bienertia cycloptera* (Chenopodiaceae) lack Kranz anatomy and have carbon isotope values like C₄ and CAM plants. Lack of nighttime CO₂ fixation indicates they are not CAM. Their photosynthetic responses to varying CO₂ and O₂ are typical of C₄ plants with Kranz anatomy. These species exhibit independent, novel solutions for the function of the C₄ mechanism through spatial compartmentation of dimorphic chloroplasts and other organelles, and photosynthetic enzymes, in distinct positions within a single chlorenchyma cell. Two inter-connected chloroplast-containing cytoplasmic compartments in the chlorenchyma cells are spatially separated.

Xylem and phloem differentiation

A general account of differentiation

Differentiation is a process at cellular level whereby a nascent unspecialised cell assumes a specialised structure and function in order to meet some specific structural or physiological requirement of the multicellular body. It is a significant process as it establishes specialised functions in different groups of cells in a multicellular body thereby bringing about division of labour which is the most important advantage of multicellular structure.

Differentiation in Plants

The differentiation process among plants is characterized by –

- It is a location dependent process rather than lineage dependent as in animals.
- Largely governed by phytohormones which may act in the short or long range. There are no separate morphogenetic factors in plants unlike animals.
- Plants differentiation involves three types of cellular specialisation –
 1. Specialisation by form transition. For eg., conversion of parenchyma into collenchyma.
 2. Specialisation by partial cellular breakdown – as in phloem sieve element cells in which nucleus, vacuole, and many protoplasmic components break down.
 3. Specialisation by Programmed Cellular Death – as found in case of xylary element formation and sclerenchymatous cells. This type of cellular specialisation is totally absent in case of animals.

Stability of Differentiation

Differentiation is essentially a stable process in plants requiring a change in gene expression pattern. However, two types of differentiation patterns have been identified on the basis of reversibility-

(a) Irreversible Differentiation or Plastic Differentiation –

- Applies to xylary elements, sieve elements differentiation and sclerenchyma differentiation
- Irreversible because a mature sieve element lacks nucleus while a mature xylary element and sclerenchymatous cell lacks protoplasm altogether.

(b) Reversible or Elastic Differentiation –

- Seen in all other examples of cellular differentiation except the above 3 and reproductive differentiation of meristem.
- Degree of reversibility is variable. It is the highest for early derivatives of meristems, green parenchymatous cells and to an extent epidermal cells in younger parts just beneath the shoot apex. Other differentiated cells show a lesser degree of reversibility.

Stages of Differentiation

In all cases, it has 3 stages –

- (a) Initiative or Inductive Stage – where a cell is initiated for differentiation almost always by a phytohormonal signal.

5 phytohormonal signals are known to cause inducing stages –

- Auxins – promote vascular and fruit differentiation.

- Cytokinin (CK) – stimulates leaf ground tissue differentiation (mesophyll formation) and along with auxins CK may also stimulate vascular differentiation.
- Gibberellins - stimulate reproductive differentiation and elaboration of the embryo.
- Ethylene – stimulates vascular differentiation and differentiation involving PCD (Programmed Cell Death). Eg. – Aerenchyma, sclerenchyma formation.
- Brasinsteroids – required for mid or late stages of vascular differentiation.

(b) Execution Stages – essentially the stages involving –

- Biochemical Changes within the cell – eg. – synthesis of new enzymes, cytoskeleton elements, new wall materials etc.
- Physiological Changes – Eg. – altered rates of photosynthesis, changed water and ionic relations, changed sensitivity towards light as morphogenetic factors, etc.
- Structural changes – Eg – Synthesis of secondary wall, wall thickening, change in cell shape, formation of or the obliteration of vacuole, etc.
- Genetic changes in terms of differential gene expression – Eg. – certain genes are stimulated while certain others are repressed such as STM, POL and WUS – genes interact to balance the rate of cell division (which enlarges the meristem) and the rate of cell differentiation in the periphery of the meristem (which decreases meristem size).

(c) Outcome Stage – When a differentiated cell type is established, depending upon its protoplasmic and nuclear status, it may or may not differentiate.

While in a higher plant most of the differentiation involves gradual or subtle changes, the differentiation of xylem and phloem elements provide the most dramatic examples of major transitions.

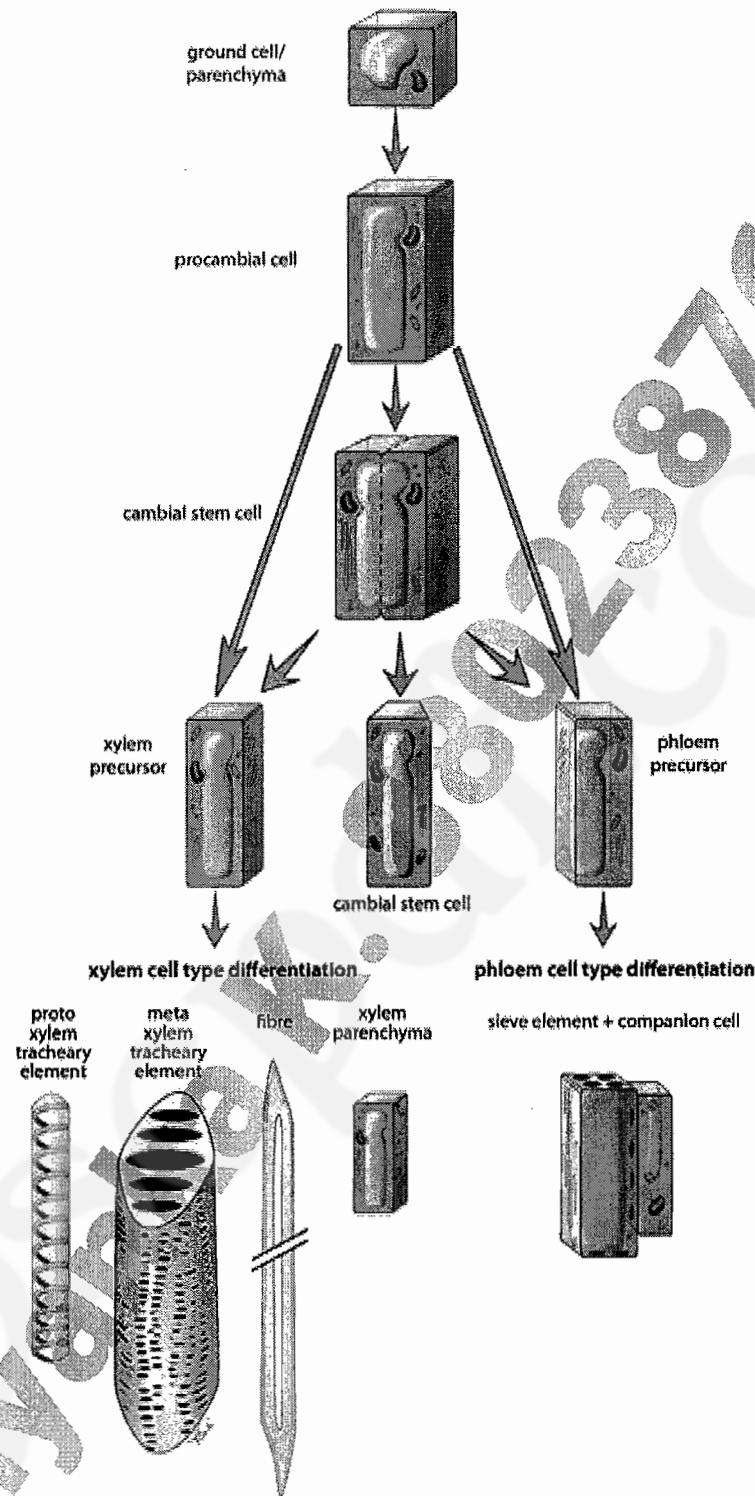


Figure: Overview of procambial/cambial cell specification and xylem/phloem cell differentiation. Procambial cells can form by the *de novo* differentiation of parenchyma cells, or by division of existing procambial cells during primary growth, thereby forming the procambium.

Xylogenesis

Xylem is the specialised tissue to conduct water and dissolved solutes from the roots to the aerial parts of the plants.

Xylem tissue has 3 elements –

- (a) Conducting elements – includes vessels and tracheary elements
- (b) Parenchyma – assists in radial translocation of water between xylem and phloem (which is essential for phloem functioning).
- (c) Sclerenchymatous Fibres – provide tensile strength to xylem tissue.

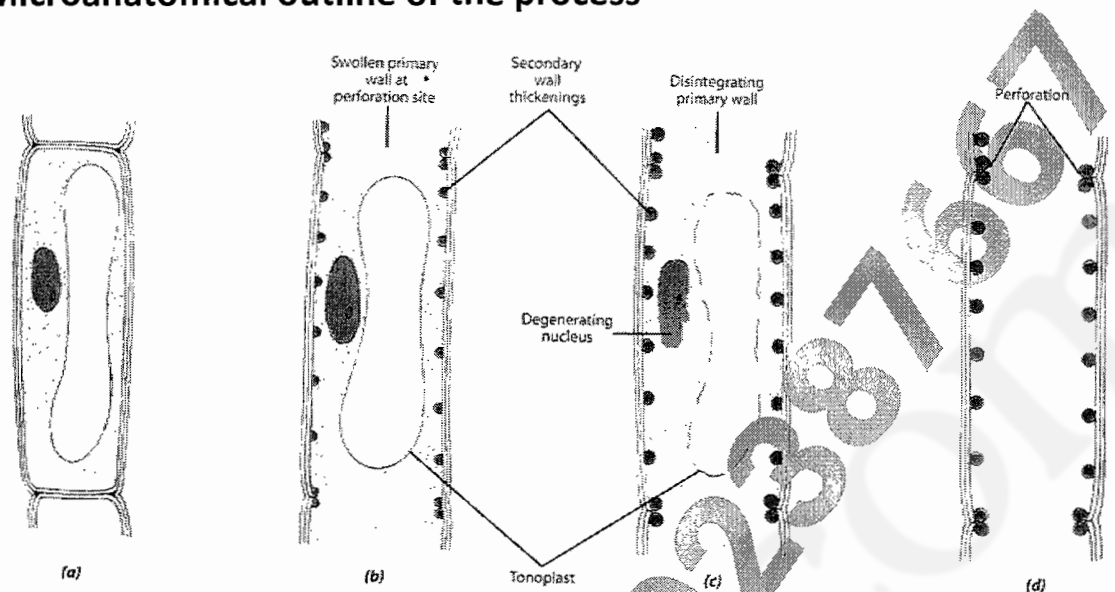
Of the above 3, the conducting elements are of highest physiological significance since they conduct water. For this task the conducting elements are microanatomically specialised.

Their specialised features are as follows.

- Absence of protoplasm – hence no obstruction in conduction.
- Thick walls with differential secondary thickening – providing rigidity and preventing wall collapse even under high values of negative pressure arising due to transpirational pull.
- Lignified walls – because of which hydrophobic properties are rendered to the wall minimising the friction in water conduction.
- Perforated region and pit formation – facilitating conduction.

Xylogenesis is a process whereby a living derivative cell arising from procambial or cambial meristem goes through a differential process involving Programmed cell Death (PCD) to generate any one type of conducting element, i.e., tracheid or vessel. It occurs since seed germination till the late stages of the plant's life span. It is a location specific process affecting only the derivatives of procambium or cambium.

Microanatomical outline of the process

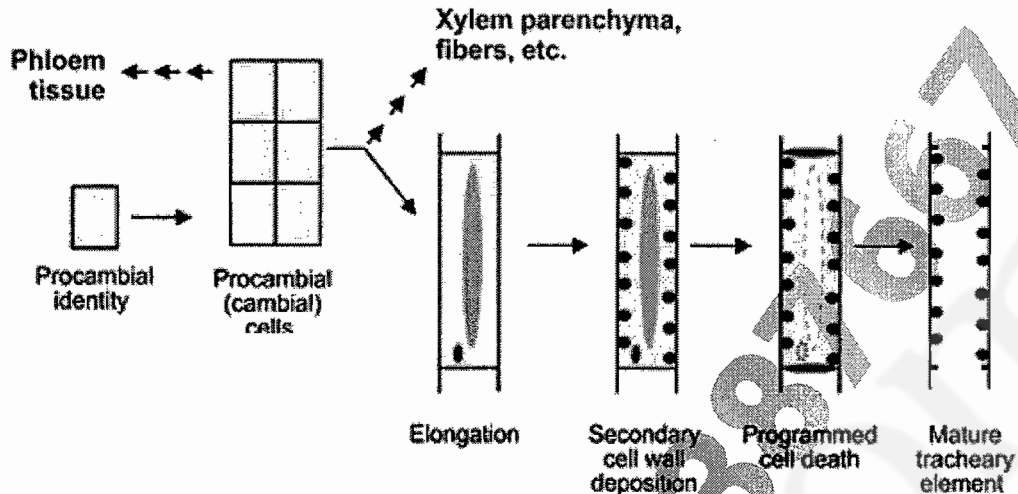


Differentiation of a vessel element (a) Young, highly vacuolated vessel element without a secondary wall. (b) The cell has expanded laterally, secondary wall deposition—in the form of a helix when seen in three dimensions—has begun, and the primary wall at the perforation site has increased in thickness. (c) Secondary wall

deposition has been completed, and the cell is at the stage of lysis. The nucleus is degenerating, the tonoplast is ruptured, and the wall at the perforation site has partly disintegrated. (d) The cell is now mature; it lacks a protoplast and is open at both ends.

The Events in Xylogenesis

Vessel elements differentiate from cells of the procambium. Vessel elements are first differentiated from other procambial cells because they expand more than their neighbors. Vessel element precursors next begin to deposit the thickened, lignified parts of their cell walls in either the ringlike, helical, netlike, or pitted pattern. The pattern can be predicted by the location of elements of the cytoskeleton within the cytoplasm that guide wall precursor to the proper location. When cell wall synthesis is complete, special wall-degrading enzymes attack the end walls of the cell, forming the perforation between adjacent elements in a vessel. Finally, the vessel elements undergo programmed cell death. The cell makes protease enzymes and nuclease enzymes that reduce proteins and nucleic acids to their simple building blocks. Surrounding parenchyma cells absorb these small molecules, leaving an empty vessel



Xylogenesis is understood in detail based on the studies conducted in vitro in tracheary element differentiation of the species *Zinnia elegans*. During in vitro studies, leaf mesophyll cells have been induced to go through the steps of xylogenesis involving 3 stages –

(a) Induction Stage –

- It initiates in immediate cambial derivative without any cell division.
- Inducing factor – Relatively high auxin concentration with respect to Cytokinin (CK) concentration. This situation arises when after cambial meristematic activity the CK levels begin to fall while auxin continues at the same level. Around this time, the levels of Brassinosteroids are also moderately high. It is believed that Auxin and Brassinosteroids have a synergistic role in Xylogenesis.
- Auxin in later stages stimulates ethylene synthesis. Ethylene, after synthesis, escapes the cells and then acts through its own

receptors. It stimulates the induction related genes. The genes activated in this stage include –

- ZeRT
- ZePT1
- ZePT2

The above 3 are the earliest genes to express after ethylene signal. The product of these genes stimulate the genes related to ribosomal protein, elongation factor proteins and tubulin proteins. Protein synthesis commences in the cambial derivative cells and it behaves almost like a dedifferentiated cell. Tubulin synthesis leads to microtubule polymerization which deposits on the inner face of primary wall and guides the deposition of the secondary wall. The late genes to be activated in the process includes – TED 2, TED 3, and TED 4 – arrest potential of the cell to divide or grow further. After this the lysis of the vacuolar membrane occurs.

(b) Execution Stage or Re-Differentiation Phase –

In this stage, following groups of protein are active –

- Proteins involved in secondary wall maturation.
- Proteins involved in wall lignification.
- Proteins related to PCD, especially, cysteine proteases, DNAses and RNAses.
- Proteins involved in enhancing enzyme activity. Eg. – Calmodulin, which works with assistance of Ca^{++} .

Experimental studies reveal that the most active hormone in execution phase is a set of Brassinosteroids.

(c) Outcome Stage –

This phase is the result of enzymatic and protein action in the execution phase. Following changes occur here –

- Thick secondary wall with lignin deposition.
- Disappearance of all the cytoplasmic compartments including nucleus.
- Breakdown of cytoplasmic materials like protein, lipid deposits, etc.
- A continuity with the cell above and cell below in case of xylary vessels due to selective breakdown of upper and lower wall material.

The linearity of xylem differentiation is maintained by a polar pattern of auxin transport which occurs from cell to cell using specialized auxin efflux proteins called PIN proteins.

The important difference between vessel and tracheary element is the presence of perforation plate in vessels. The perforation plate is the region where neither primary nor secondary wall is present.

Phloem Differentiation

Phloem is the principal tissue in vascular plants to carry out the conduction of organic solutes including photosynthetic products and various organic substances of physiological substances such as hormones like Gibberillic Acid and defense compounds Systemins.

At maturity phloem tissue has 3 elements -

- (a) **Conducting Elements** includes sieve elements (responsible for long distance transportation of organic solutes) and companion cells which are

sister cells to sieve elements and responsible for loading the organic solutes into the sieve tube element). Companion cells are absent in Gymnosperms but substituted analogously by Albuminous cells also called Strassburger Cells which are not sister structures to the sieve cells.

- (b) **Phloem Parenchyma** responsible for lateral conduction of water between phloem and xylem.
- (c) **Phloem fibres** responsible for providing structural stability.

The discussion of phloem differentiation primarily focuses upon the formation of differentiated sieve tube element cell.

Anatomically, the processes include:

1. Pronounced cell elongation and the acquisition of a characteristic bone-like shape by cells
2. Controlled loss of the nucleus and several other organelles
3. Sieve plate formation

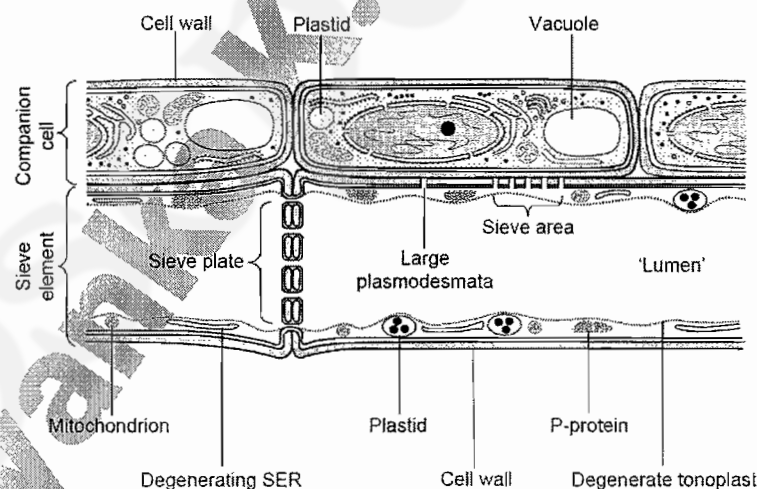
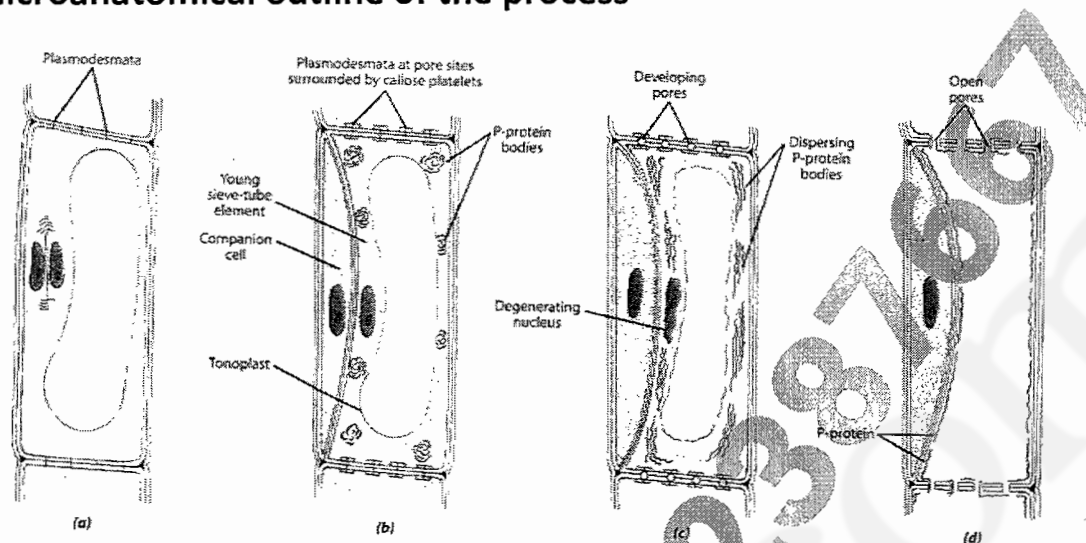


Figure: Phloem sieve tube element and companion cell

Microanatomical outline of the process



Differentiation of a sieve-tube element (a) The mother cell of the sieve-tube element undergoing division. (b) Division has resulted in formation of a young sieve-tube element and a companion cell. After division, one or more P-protein bodies arise in the cytoplasm, which is separated from the vacuole by a tonoplast. The wall of the young sieve-tube element has thickened, and the sites of the future sieve-plate pores are represented by plasmodesmata. Each plasmodesma is now surrounded by a platelet of callose on either side of the wall. (c) The nucleus is degenerating, the tonoplast is breaking down, and the

P-protein bodies are dispersing in the cytoplasm lining the wall of the sieve-tube element. At the same time, the plasmodesmata of the developing sieve plates are beginning to widen into pores. (d) At maturity, the sieve-tube element lacks a nucleus and a vacuole. All of the remaining protoplasmic components, including the P-protein, line the walls, and the sieve-plate pores are open. The callose platelets were removed as the pores widened. Not shown here but also present in the mature sieve-tube element are smooth endoplasmic reticulum, mitochondria, and plastids.

The process of phloem development can be subdivided into 3 phases of morphogenesis:

Induction Phase

- Events of this phase are morphologically indistinguishable but at the biochemical level the sieve tube mother cell is stimulated to undergo the execution stages.
- All the stimulating factors are not characterized but an increasing concentration of sucrose with constant level of auxin tends to favour phloem differentiation.
- During this activity the *ALTERED PHLOEM DEVELOPMENT (APL)* gene is activated which tends to repress ethylene synthesis and thus prevents the onset of PCD.
- Another gene called *PHLOEM POLARITY (PP)* gene, stimulates the process of longitudinal cell division. With this execution phase begins.

Execution Phase

- This phase has not been characterized in detail with respect to the molecular elements but there are certain drastic morphological changes which occur during this phase. Most of the morphological changes are outcome of partial breakdown of protoplasmic material without leading to complete PCD.
- In this process, hydrophilic glycoproteinous globular proteins called **P-proteins** also play important role in wall differentiation.
- At this stage *PHLOEM DIFFERENTIATION 1-5 (PD1-PD5)* are most active.

Outcome Phase

- Culmination of execution phase results into a mature sieve tube cell which is connected to upper and lower sieve tube cell via sieve plate regions which are perforated end walls.
- Fully formed phloem tissue now participates in organic solute translocation by a pressure flow mechanism.

Secondary growth in stem and wood anatomy

Vascular cambium

The vascular cambium is the meristem that produces the secondary vascular tissues. It is a lateral meristem, for in contrast to the apical meristems, which are located at the tips of stems and roots, it occupies a lateral position in these organs. The vascular cambium, like the apical meristems, consists of initial cells and their recent derivatives. In the three-dimensional aspect, the vascular cambium commonly forms a continuous cylindrical sheath about the xylem of stems and roots and their branches.

When the secondary vascular tissues of an axis are in discrete strands, the cambium may remain restricted to the strands in the form of strips. Later, these cambial strips are joined to form a continuous ring. (Fig. 1)

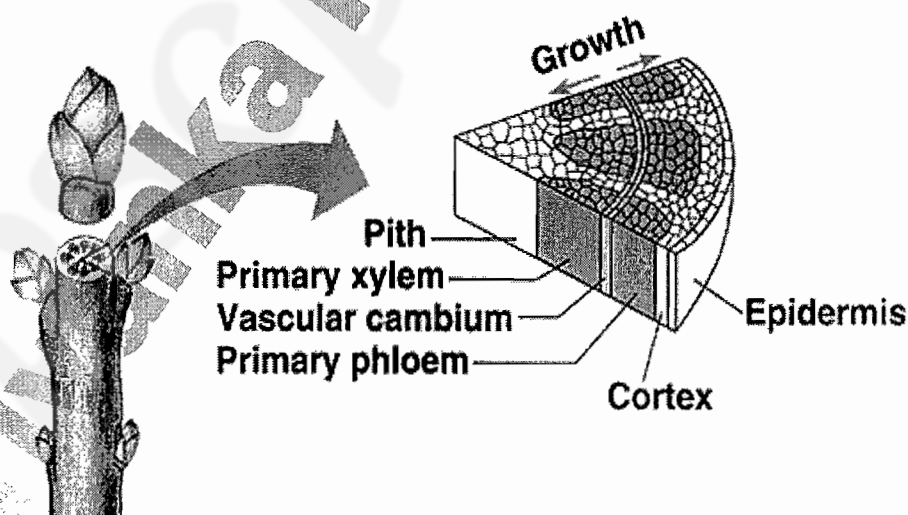


Figure 1: Position of vascular cambium just before the onset of secondary growth

The cells of the vascular cambium

The cells of the vascular cambium do not fit the usual description of meristematic cells, as those that have dense cytoplasm, large nuclei, and an approximately isodiametric shape. Although the resting cambial cells are densely cytoplasmic, they contain many small vacuoles. Active cambial cells are highly vacuolated, consisting essentially of a single large central vacuole surrounded by a thin, peripheral layer of dense cytoplasm.

The vascular cambium contains two types of initials: **Fusiform Initials** and **Ray Initials**.

Morphologically, cambial initials occur in two forms. One type of initial, the fusiform initial, is several times longer than wide; the other, the ray initial, is slightly elongated to nearly isodiametric. The term fusiform implies that the cell is shaped like a spindle. A fusiform cell, however, is an approximately prismatic cell in its middle part and wedge-shaped at the ends.

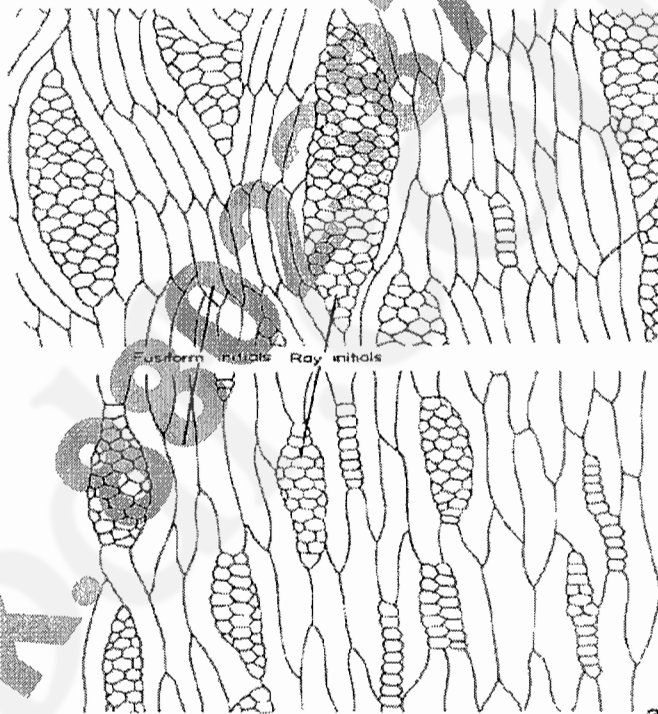


Figure 2: Fusiform Initials and Ray Initials

The fusiform initials give rise to all cells of the xylem and phloem that are arranged with their long axes parallel to the long axis of the organ in which they occur; in other words, they give rise to the longitudinal or axial systems of xylem and phloem. Examples of elements in these systems are tracheary elements, fibers, and axial parenchyma cells in the xylem; sieve elements, fibers, and axial parenchyma cells in the phloem.

The ray initials give rise to the ray cells, that is, the elements of the radial system (the system of rays) of the xylem and the phloem.

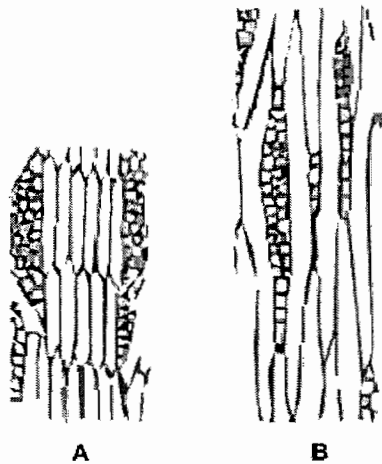


Figure 3: A. Storied Cambium; B. Non-storied Cambium

The cambium may be **storied** (stratified), or **nonstoried** (nonstratified), depending on whether or not, as seen in tangential sections, the cells are arranged in horizontal tiers. In a storied cambium the fusiform initials are arranged in horizontal tiers, with the ends of the cells of one tier appearing at approximately the same level (Fig. 3). It is characteristic of plants with short fusiform initials. Nonstoried cambia are common in plants with long fusiform initials, which have strongly overlapping ends. Intergrading types of arrangement occur in different plants. The cambium of *Fraxinus excelsior* is a mosaic of storied and nonstoried local areas.

Formation of secondary xylem and secondary phloem

When the cambial initials produce xylem and phloem cells they divide periclinally. At one time a derivative cell is produced inwardly toward the xylem, at another time outwardly toward the phloem, although not necessarily in alternation. Thus each cambial initial (Fig. 4) produces radial files of cells, one toward the inside, the other toward the outside, and the two files meet at the cambial initial.

These cambial divisions, which add cells to the secondary vascular tissues, are also called **additive divisions**.

During the height of cambial activity, cell addition occurs so rapidly that older cells are still meristematic when new cells are produced by the initials. Thus a wide zone of more or less undifferentiated cells accumulates. Within this zone — the **cambial zone** — only one cell in a given radial file is considered to be an initial in the sense that after it divides periclinally, one of the two resulting cells remains as an initial and the other is given off toward the differentiating xylem or phloem.

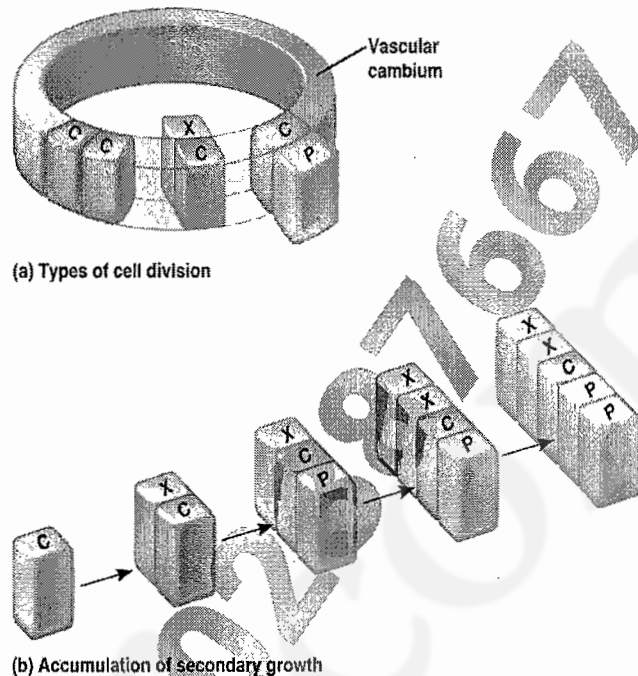


Figure 4: Additive divisions of the cambium

The initial is the only cell able to produce derivatives toward both the xylem and the phloem.

Sanio recognized distinct groups of four cells in the cambial zone. Now called **Sanio's four**, each group of four cells consists of the initial, its most immediate derivative, and two daughter cells. When xylem is being formed, the daughter cells divide once more, producing four xylem cells, referred to as the expanding, or enlarging, four. The presence of Sanio's four in the cambial zone and of groups of expanding four in the differentiating xylem of conifers has been confirmed. Groups of four have not been recognized on the phloem side of the cambium; there, the cells appear to occur in pairs.

The divisions increasing the number of initials are called **multiplicative divisions** (Bannan, 1955). In species having storied cambia (cambia that have short fusiform initials), the multiplicative divisions are mostly radial anticlinal.

Thus two cells appear side by side where one was present formerly, and each enlarges tangentially. In herbaceous and shrubby eudicots the anticlinal divisions are frequently lateral; that is, they intersect twice the same mother cell wall. In species having nonstoried cambia (cambia with long initials), the initials divide by formation of more or less inclined, or oblique, anticlinal walls (pseudotransverse divisions), and each new cell elongates by apical intrusive growth.

Multiplicative division of the cambium increases the circumference of the cambial ring in tune with the growth of the stele.

Thus, the secondary growth of stem (or roots) is the result of the activity of the vascular cambium, which occurs in between xylem, and phloem of each vascular bundle. It must be noted that towards the beginning of secondary growth there is a process of dedifferentiation in some of the parenchyma cells of the medullary rays, adjoining the vascular cambium. As a result, these cells now become meristematic and represent the inter-fascicular cambium. The meristematic cells in the intra-fascicular cambium and inter-fascicular cambium fuse and result in the formation of a continuous strip of meristem called **cambial ring** (Figure 5).

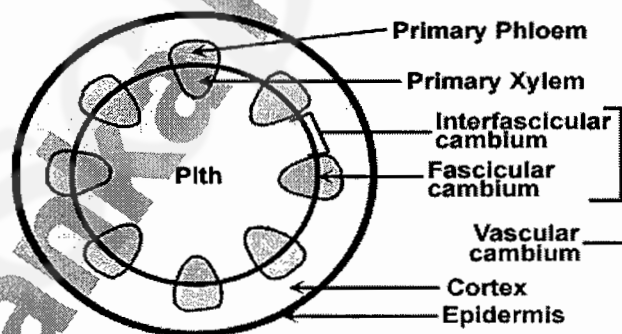


Figure 5: The meristematic cells in the intra-fascicular cambium and inter-fascicular cambium fuse and result in the formation of a continuous strip of meristem called **CAMBIAL RING**

Secondary Growth in Monocots

Secondary growth is usually absent in monocots as they do not possess a vascular cambium like that of dicots. Yet, there are certain distinct types of mechanisms causing thickening of the stem axis in monocots. They are reviewed below in brief.

In Palms

In arborescent forms, such as palms and other species with similar growth habit, increase in diameter is accomplished by **primary thickening meristem (PTM)**.

This meristem originates below the region of attachment of the young leaf primordia by periclinal division of the cells. In longitudinal section, it appears in the form of a flat or concave zone of several layers of rectangular cells oriented parallel to the surface of the stem. At first, the young stem increases mainly in width by the activity of the PTM but in later stages it is also responsible for increase in height of the stem.

In some palms, expansion of the ground tissue continues in the older part of the stem where parenchyma cells undergo division and cell expansion and the intercellular spaces also increase in size. This type of growth – called **Diffuse Secondary Growth**.

In woody Monocots – Dracaena, Yucca, etc

In some woody Liliiflorae, such as *Agave*, *Dracaena* and *Yucca* and Xanthorrhoeaceae – secondary growth brought about by a special type of vascular cambium.

This cambium is in continuation with the PTM and develops in the parenchyma outside the primary vascular bundles.

Unlike the vascular cambium of dicots, this meristem produces entire secondary vascular bundle, comprising both xylem and phloem, in localized regions by

active divisions of the cells in various planes and parenchymatous ground tissue – known as **Conjunctive tissue** – towards the inner side and only a little parenchyma towards the outer side. The secondary vascular bundles may be amphivasal (eg – *Dracaena*) or collateral (eg – *Kingia*), and usually occur in more or less distinct radial files.

Usually cells from many tiers of cambium contribute in the production of a secondary vascular bundle.

The xylem of secondary bundles – composed of tracheids only. In most monocots, tracheids on the inner side (proximal) of the bundle start developing thickenings before all divisions are complete. But this is not true for all monocots, such as in *Aloe arborescence*, the bundle is completely differentiated before any of the elements have developed even slight thickenings.

In some monocots, such as *Aloe* and *Cocos*, a periderm like that of dicots is formed, whereas in others the protective tissue is developed in the form of a storied cork.

Secondary growth in cortex

It is the result of the activity of a secondary meristem called **cork cambium**, which appears between hypodermis and primary cortex. Some of the parenchyma cells in the peripheral layers of cortex undergo dedifferentiation and become meristematic. These cells now represent the cork cambium or **phellogen**. The cork cambium starts exhibiting mitotic activity on both the sides, just as the cambial ring in the stele.

The mitotic activity on the inner surface of the cork cambium results in the formation of cells, which undergo differentiation into a living tissue, called secondary cortex or **phelloderm**, just above the primary cortex. The mitotic activity on the outer surface results in the formation of cells, which undergo differentiation into a dead tissue, called cork or **phellem**, just below the

epidermis. The cork covers and masks the hypodermis. The tissue resulting from secondary growth in the cortex the cork, the cork cambium and the secondary cortex-together represent a region called **periderm**.

The periderm along with the primary cortex represents the **bark**. In several dicot plants, the bark peels off regularly.

Due to the formation of periderm, the epidermis is subjected to pressure and as a result it breaks at several places to form openings called **lenticels**. The lenticels, also known as aerating pores, enclose a group of living cells called complementary cells. Through these cells exchange of respiratory gases and to some extent transpiration take place.

Thus, secondary growth in the cortex results in the formation of periderm. Due to the addition of this region there is an increase in the girth of the cortex.

Box 1: Types of bark

- **Ring bark.** Where a stem has concentric successive periderms (entirely cylindrical), a tight or smooth bark can develop.
- **Scaly bark.** Where a stem has discontinuous, overlapping successive periderms, patches of bark will form and can be shed. This is generally termed a scaly bark.
- **Fissured bark.** Fissured bark has a net-like pattern from splitting of the outer and inner bark. Many trees with fissured bark have well-developed secondary phloem fibers in the inner bark (bast fibers), which formerly were widely used for making cordage and paper, give the trunk a very strong cover. Fibers would, on the one hand, give added strength for bending and limit stress on sieve tubes while also protecting the sugar-conducting sieve tubes of phloem, blocking sucking or burrowing insects. Fibrous barks are not necessarily fissured, as in many species of figs (*Ficus*).
- **Smooth bark.** Smooth barks can be smooth and very glossy to dull. Generally these have a very thin outer bark.
- **Peeling bark (exfoliating).** Especially for ring bark species, occurrence of thick-walled cells alternating with thin-walled cells causes barks to separate like thin wrappers, peeling or exfoliating from where a layer breaks (*Bursera*, examples one type and another view and another view; *Prunus*, *Betula*, certain *Jatropha*). Peeling barks of eucalyptus species (examples: *E. maculata*, *E. citriodora*, *E. deglupta*, versus a nonshedding ironbark) occur because layers of bark separate where there is thin-walled phloem parenchyma. Shagbark hickory (*Carya ovata*) has peeling strips of fibrous bark. Species of *Melaleuca* (Examples: one species and another view and *M. styphelioides*) and *Callistemon* (family Myrtaceae) often have exfoliating layers like paper. Some species of legumes also have peeling bark.
- **Cracked bark.** As a tree increases in girth, great tension on the bark can cause vertical and horizontal cracking. Cracks may develop along planes of stress or more simply outline boundaries of scaly bark.
- **Furrowed cork.** The cork oak (*Quercus suber*) and a number of other trees (*Cussonia spicata*, *Erythrina latissima*, and *Phellodendron*) have deeply furrowed bark with thick accumulation of cork cells. These cork cells tend to have thin-walls and are filled with air. Corky outer bark

may also appear in longitudinal arrangements or wings (*Casuarina*, *Aristolochia*, and *Zanthoxylum*).

- **Green stems.** Species with photosynthetic stems almost always are able to capture sufficient sunlight when development of the opaque initial periderm is delayed or totally suppressed. A stem can contribute significantly to total carbon uptake of the plant only if stomates are present at a substantial density, and can remain functional over several years.
 - Stem succulents, such as cacti and euphorbs, have a long delay in the initiation of periderm. These stems do not tear or split because the epidermis undergoes extra cell divisions during its formation for increasing the surface area. Instead, periderm formation occurs primarily in response to stress and injury, e.g., sun damage along rib margins. When periderm forms, it typically arises from the outermost layer of cortex and requires a long time to encircle the axis. In many arborescent cacti, for example, only the trunk is fully covered by scaly bark.
 - Photosynthetic old stems, such as palo verdes (*Cercidium* and *Parkinsonia aculeata*), over many years experience cell divisions of the epidermis, cortex, and phloem, thereby increasing stem surface area while stem circumference increases without disturbing the operations of the stomates. Even a fully mature palo verde may have very little bark formation on the trunk. Many shrubs of desert and semiarid habitats have photosynthetic stems that remain green for several years before developing the initial periderm.
 - Many families with both herbs and shrubs have woody species with thick stems that are partially green for more than a year. Especially herbaceous plant groups tend to show a long delay in full acquisition of bark (example: *Tithonia diversifolia*).
 - Certain bottle trees form green trunks that very slowly develop stripes or patches of periderm (*Ceiba* and other Bombacaceae, examples *Pseudobombax* and another view and *Fouquieria columnaris*, *Brachychiton rupestris*). There may, in fact, be no carbon uptake by these green stems, because they lack functional stomates, but green tissues can obtain energy via the light reaction and recycle internal carbon dioxide, which was generated by cell respiration of the bark cells. Even a fully mature tree may still have patches of green on the trunk.
 - Some species possess smooth, tight or peeling, thin, nearly transparent outer bark hiding a deeper layer of green, photosynthetic tissue. These species do not appear to have photosynthetic stems, because the surface bark is tan to red (examples: *Bursera*, *Pachycormus*, *Jatropha* spp.).
- **Corky wings.** One diagnostic character is the presence of corky wings on young stems. In some cases, wings are due to stimulation of localized phellogens along a stem angle, as in winged euonymus (*Euonymus alatus*). Wings also occur on young stems of sweet gum (*Liquidambar*). Longitudinal splitting is the cause of stem wings in certain species of elm (*Ulmus*).
- **Monocotyledonous periderm.** Certain arborescent species, e.g., *Cordyline terminalis*, *Beaucarnea stricta*, *Dracaena draco*, and *Yucca*, segments of suberized cells appear but without having a special cambium. This is termed storied cork. *Aloe bainesii* and other arborescent aloes have a scaly to exfoliating type of surface layers. In palms, the outer cells of the trunks become heavily lignified, and a few palm species (*Livistona*) also have suberin deposited in surface cell walls. No monocotyledon has a true periderm as found in dicotyledons and gymnosperms.
- **Bark armature.** Bark on old stems and trunks may have formidable armature in the form of heavy, persistent bark prickles (also called bark emergences). Examples are found in Bombacaceae (*Chorisia speciosa*; *Ceiba aesculifolia* and another view), *Zanthoxylum* (one example and another view), and certain Sapotaceae. Stipular spines may also persist on old stems.

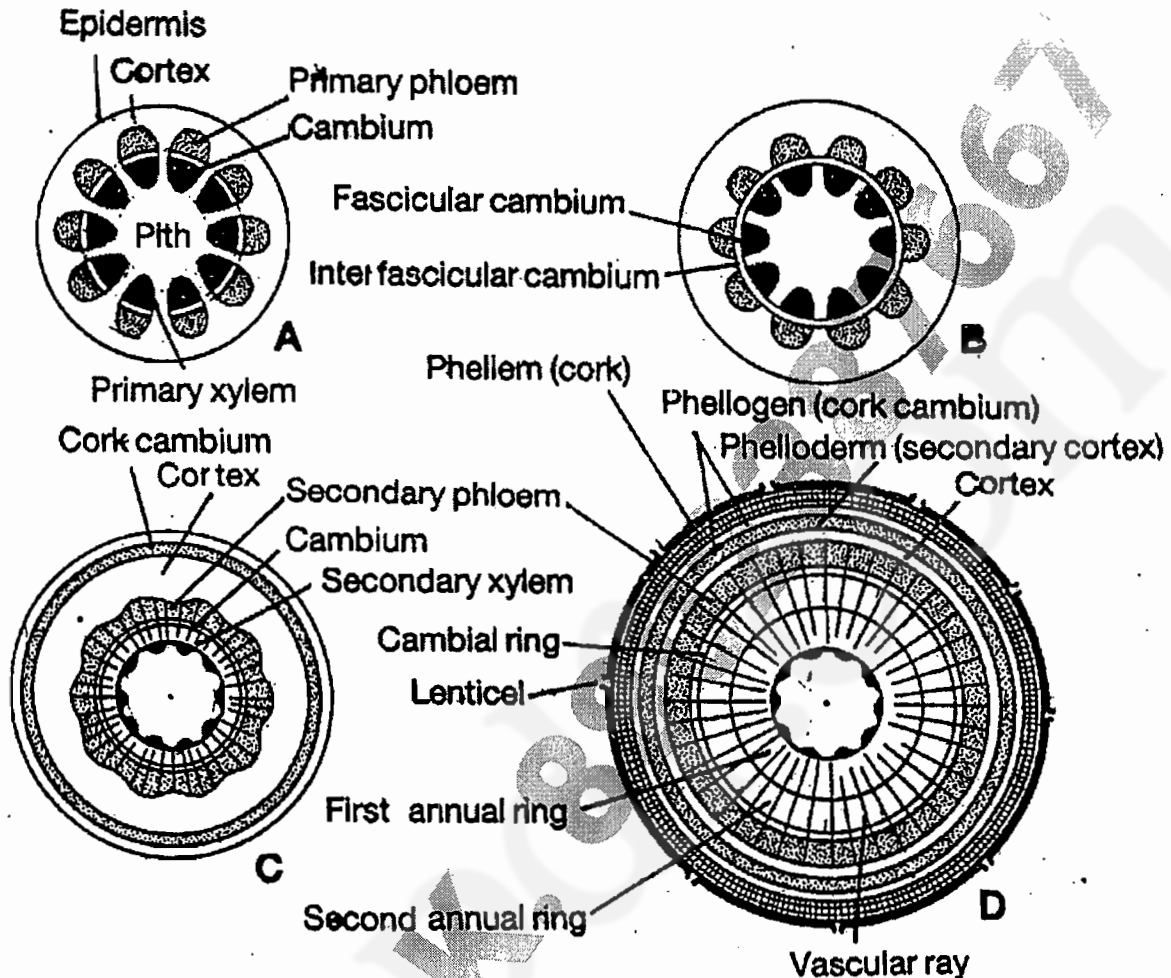


Figure 6: Schematic representation of various stages of secondary growth in a dicot stem

Wood anatomy

All cells formed to the interior of the vascular cambium develop into secondary xylem. It is known as **wood**. Secondary xylem contains all the types of cells which occur in primary xylem but no new type of cells. Thus, wood contains the following cell types.

1. Tracheids
2. Vessel elements (found only in Angiosperms and the Gymnospermic genus *Gnetum*)
3. Fibers and sclereids
4. Parenchyma

The arrangement of secondary xylem cells reflects that of the fusiform and ray initials. There are two types of systems or orientations in which the cells are arranged in the wood.

1. An axial system, which is oriented along the long axis of the plant, is derived from the fusiform initials.
2. A radial system, whose cells are arranged in the radial orientation of the plant axis, develops from the ray initials.

Axial System of the Wood

The axial system always contains elongated cells, mainly the tracheary elements, which are tracheids or vessel elements or both. The tracheary elements carry out longitudinal conduction of water through the wood. In many species of woody angiosperms, the axial system also contains fibers that give the wood strength and flexibility. Most commercially important angiosperm woods contain large amounts of fibers, making them strong, tough, and useful for construction. They are called **hardwoods**, a term now used for wood of all basal angiosperms and eudicots, even those that lack fibers or are very soft, such as balsa.

Hardwoods have vessels for conducting sap upward. Vessels are a series of relatively large cells with open ends, set one above the other and forming open passages for long distances. In most hardwoods, the ends of the individual cells are entirely open. The size, shape, and arrangement of pores vary considerably between species, but are relatively constant within a species.

Woods from conifers such as pines and redwoods have few or no fibers and thus have a softer consistency. These are known as the **softwoods**, even though in many instances (such as bald-cypress, *Taxodium*) they are actually much harder than many hardwoods. Because softwoods do not contain vessel cells, the tracheids serve the dual function of transporting sap vertically and giving strength to the wood. Softwood fibers range from about 0.1 to 0.3 in. (3 to 8 mm) in length. Fibers and parenchyma cells are sparse or absent in most of the soft woods.

The two kinds of wood have basic structural differences, but the terms “softwood” and “hardwood” do not accurately express the relative density (weight per unit volume) or hardness of the wood. For example, one of the lightest and softest woods is balsa (*Ochroma lagopus*), a tropical hardwood. By contrast, the woods of some softwoods, such as slash pine (*Pinus elliotii*), are harder than some hardwoods.

The complexity of the axial system of wood varies greatly, for example in many species, some immature cells of axial system undergo transverse divisions and differentiate into columns of xylem parenchyma. This is axial xylem parenchyma, and it is important as a temporary reservoir of water. Many desert-adapted trees have abundant xylem parenchyma. In contrast, conifers such as pine, cedar, juniper, and redwood have little or no axial parenchyma and therefore have little reserve water. For them, tough, waxy, water-conserving leaves are selectively advantageous.

Some angiosperms, especially some basal angiosperms such as in family Winteraceae, have mostly just tracheids; however, in the majority of woody angiosperms, all possible types of cells are present.

The Radial System of Wood

The radial system of wood is usually simple. In woody angiosperms, it contains only parenchyma, arranged as uniseriate, biseriate, or multiseriate masses called rays. Ray parenchyma cells store carbohydrates and other nutrients during dormant periods and conduct material over short distances radially within wood. The two basic types of ray parenchyma cells are:

1. upright cells
2. procumbent cells.

In some plants, procumbent ray cells have no direct connection with axial cells, but upright cells do. The ray/axial interface can take many forms. If the upright ray parenchyma cell is adjacent to axial parenchyma, plasmodesmata occur. If

the ray parenchyma is adjacent to an axial tracheid or vessel element, the tracheary element has pits in its secondary wall and the ray cell has very thin walls facing the pits. In early springtime, when trees such as maples are drawing on their nutrient reserves, the starch that had been stored in the upright cells is the first to be digested into sugar and passed into the axial tracheary elements for conduction to newly expanding buds, leaves, and flowers. Starch in procumbent cells is not digested initially. It must first be routed through upright cells for transfer to axial conducting cells.

In gymnosperms, xylem rays are uniseriate; they are multiseriate only if they contain a resin canal. In addition to ray parenchyma cells, they may contain ray tracheids-horizontal, rectangular cells that look somewhat like parenchyma cells but have secondary walls, circular bordered pits, and protoplasts that degenerate quickly after the secondary wall is completed.

Ring porous and Diffuse porous wood

The word porous is used by the wood anatomist to refer to the appearance of the vessels in transverse sections. Diffuse-porous woods are woods in which the vessels, or pores, are rather uniform in size and distribution throughout a growth ring. In ring-porous woods the pores of the earlywood are distinctly larger than those of the late-wood, resulting in a ring-like zone in the earlywood and an abrupt transition between the earlywood and late-wood of the same growth ring. Intergrading patterns occur between the types, and woods showing an intermediate condition between ring-porous and diffuse-porous may be called semi-ring porous or semi-diffuse porous.

In ring-porous trees the vessels laid down at the beginning of the growing season are much larger than subsequent vessels laid down at the end of the season (or ring). Diffuse-porous trees form vessels of roughly the same radial diameter throughout the growing season.

Ring porous

Carya pecan (pecan)

Castanea dentata (American chestnut)

Fraxinus americana (white ash)

Gleditsia triacanthos (honey locust)

Morus rubra (red mulberry)

Quercus spp. (deciduous oaks)

Semi-ring porous or semi-diffuse porous

Diospyros virginiana (persimmon)

Juglans cinerea (butternut)

Quercus virginiana (live oak)

Salix nigra (black willow)

Diffuse porous

Acer saccharinum (silver maple)

Aesculus glabra (buckeye)

Betula nigra (red birch)

Fagus grandifolia (American beech)

Magnolia grandiflora (evergreen magnolia)

Tilia americana (basswood)

Annual Rings in Wood

In regions with strongly seasonal climates, the vascular cambium is quiescent during times of stress, either winter cold or summer drought, but when quiescence ceases, the vascular cambium becomes active and cell division begins. At the same time, the new, expanding leaves are thin and delicate, and their cuticle is neither thick nor fully polymerized. Leaves like this lose water at a rapid rate, and thus, trees need a high capacity for conduction at this time.

The first wood formed is **early wood**, also called **spring wood**, and it must have a high proportion of wide vessels or, in gymnosperms, wide tracheids.

Later, the cuticle has thickened, transpiration is less, and large numbers of newly formed vessels are conducting rapidly. Wood produced at this time, called **late wood** or **summer/autumn wood**, can have a lower proportion of vessels. Late wood is stronger if it contains numerous fibers or, in gymnosperms, if it contains narrow, thick-walled tracheids. Finally, at the end of the growing season, the cambium becomes dormant again. The last cells often develop only as heavy fibers with especially thick secondary walls.

In a tree of temperate region, it is easy to see early wood and late wood, the two together making up 1 year's growth, an **annual ring**.

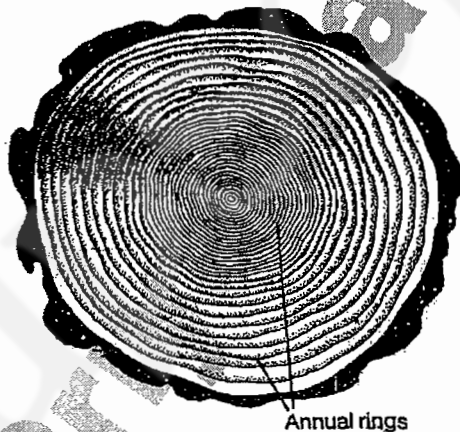


Figure 7: TS of an old dicot wood showing annual rings

An alternative arrangement exists in tropical trees. In some tropical species, vessels form throughout the growing season. Those produced in spring are neither more abundant nor obviously wider than those pro-

duced in summer. Because the wood of a growth ring has vessels located

throughout it, it is said to be diffuse porous, whereas species with vessels

restricted mainly to early wood are ring porous. Examples of trees with diffuse porous wood are yellow birch, aspen, and sugar maple and trees with ring porous wood include red oak, sassafras, and honey locust.

In mild tropical climates, the cambium may remain active almost continuously, and the wood of one year is difficult to distinguish from that of another; growth rings are indistinct.

Heart Wood and Sap Wood

The center of a log is almost always darker in color than the outer wood, and it is usually drier and more fragrant. The dark wood is **heartwood** and the lighter, moister outer region is **sapwood**.

The different regions exist because vessels and tracheids do not function forever in water conduction; water col-

umns break because of freezing, wind vibration, tension, woodboring insects, and other factors. After the water column breaks, vessels and tracheids in which this has occurred usually never conduct water again.

New water-filled tracheary elements are produced by the cambium during the next year, which makes the sap wood.

The inner wood parenchyma cells undergo numerous metabolic changes and produce large quantities of phenolic compounds, lignin, and other dark-colored, aromatic substances that inhibit growth of bacteria and fungi. These chemicals are usually dark and aromatic, and as they accumulate, wood becomes darker and more fragrant, such as cedar wood. Ultimately, all parenchyma cells die, and conversion of sapwood to decay-resistant heartwood is complete.

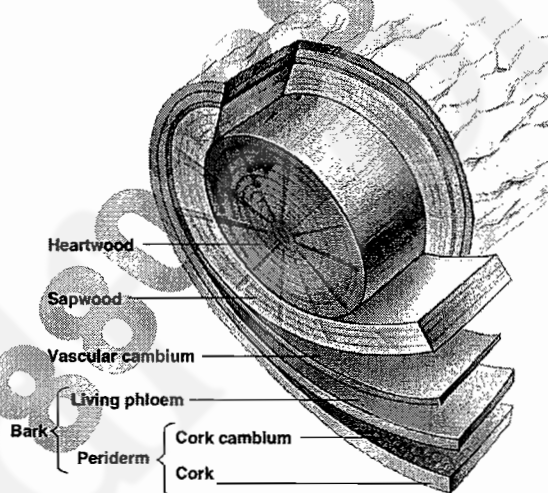
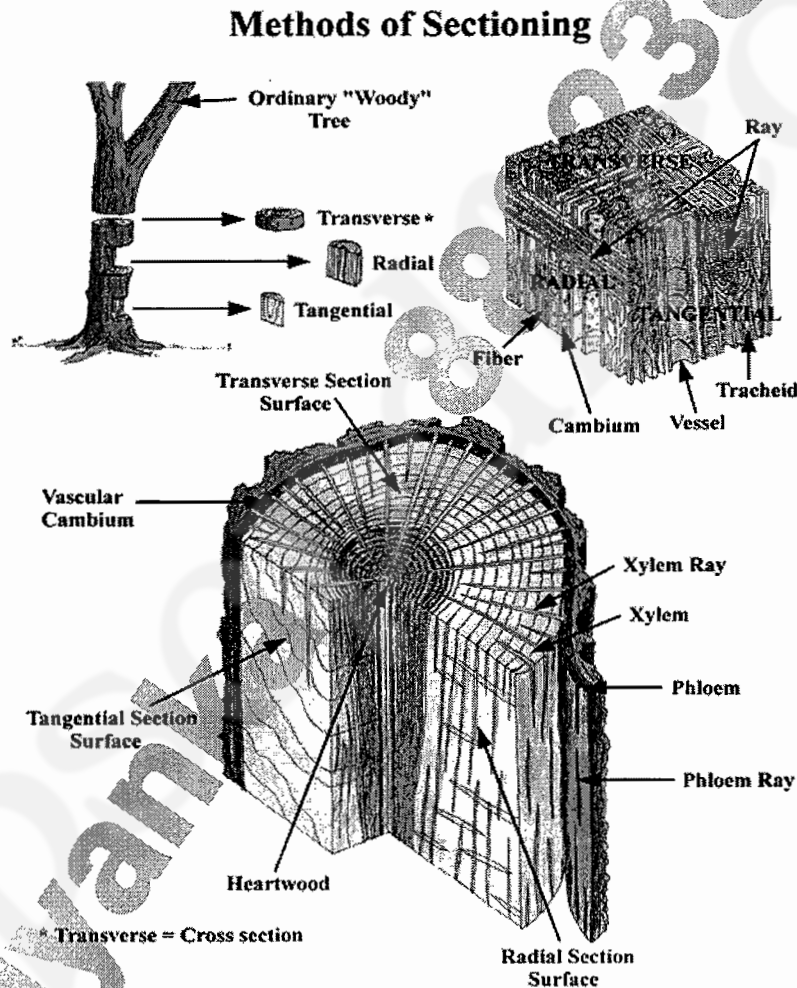


Figure 8: Heart wood and sap wood

A new layer of sapwood is formed each year by the vascular cambium, and on average, one annual ring is converted to heartwood each year. Thus, whereas heartwood becomes wider with age, sapwood has a more or less constant thickness.

Appendix: Methods of wood sectioning



Anomalous Secondary Growth

The process of secondary growth in angiosperms has often been categorized as "Normal" and "Anomalous". The following features characterize normal secondary growth in angiosperms:

1. Presence of a single cambial ring
2. Presence of a complete cambial ring by the formation of inter-fascicular cambium.
3. Localization of the cambium strictly between the primary xylem and the primary phloem.
4. Formation of the secondary phloem towards the outer side and secondary xylem towards the centre.
5. Presence of the interfascicular cambium at the same level as the cambial strip.
6. Only a single ring of cork cambium in the extra-stelar region.
7. Presence of all the essential elements of the secondary xylem
8. The meristematic activity of the cambial ring in the stelar region is uniform throughout. This results in the uniform increase in girth or diameter of dicot stems (and of dicot roots). Therefore, their outline becomes cylindrical or circular in cross-section.

When the secondary growth process in the angiosperms does not fulfill anyone or more of the above criteria, it is regarded as anomalous.

Classically, the term anomalous secondary growth has been used to indicate the forms of cambial activity that deviate from that commonly found in conifers and woody dicotyledons of the temperate regions (K. Esau, 1976).

Reasons for Anomaly in Secondary Growth

Anomaly in the secondary growth process can occur by anyone or more of the following factors.

1. Unusual position of the cambium
2. Abnormal cambial behaviour
3. Formation of more than one cambial ring
4. Presence of extra-stelar cambium
5. Secondary development in the monocots

The Ecological Types of Anomalous Secondary Growth

As the plants are subjected to different environmental conditions, the anomalous secondary growth may or may not be adaptive.

ADAPTIVE OR ENVIRONMENTAL

Anomalous secondary growth in climbers, lianas and storage organs (e.g., beetroot, turnip root) is environmental as these plants are morpho-physiologically different from normal types. Hence, anomalies in these plants are adaptive.

NON-ADAPTIVE

In some members of Nyctaginaceae, Amarantaceae, Chenopodiaceae, Oleaceae, etc., the anomalous secondary growth is non-adaptive, as that has nothing to do with the adjustment of plants in the prevailing environmental condition. Here the anomaly in secondary vascular structures is attributed to the abnormal activity of cambium which is normal in disposition.

The Types of Anomalous Secondary Growth Based on Origin

Anomalous Position of Cambium

Stems of several unusual shapes or types are formed by the unusual position of the cambium. For example in *Thinouia scandens* while the stem is young, the cambium is thrown into folds or ridges. Here, the tips of the ridges are pinched off and after separation develop *steles* in them.

In *Bauhinia langsdorffiana*, a somewhat similar structure is formed as described above. The structure is brought about by the breaking into strips of the original cambium cylinder, and even of the vascular cylinder formed by this cambium, by the proliferation of xylem parenchyma. The parenchyma in the xylem and phloem increases excessively, thus rupturing the first-formed, original tissues and the cambium sheet, which formed them.

In *Serjania ichthyoctona*, the cambium appears originally in several separate strips. Each of which surrounds portions, even individual strands, of the primary xylem and phloem. This type of stem appears to be made up of several fused stems. In the older stems, this compound condition becomes more marked, because the parts are separated from each other. In this way there is formed a stem composed of strands lying together more or less like the strands of a rope.

Abnormal behaviour of normally placed cambium

Sometimes when the normal cambium starts cutting cells at several places irregularly, and forms at certain places much larger portions of xylem than of phloem, and at other places, more phloem than xylem, and a ridged and furrowed xylem cylinder is produced. This may be of simple structure (e.g., some Bignoniaceous genus) or very complex (e.g., in *Bignonia* sp.). The following types of anomalous stems are known to develop due to unusual activity of cambium.

Presence of Fissured Xylem. The fissured xylem may only be seen in old stems. First wedges of phloem are formed and thereafter the xylem strand become fissured by dilation and cell division in wood parenchyma and pith.

In *Aristolochia*, segments of the cambium cut only parenchyma cells both on outer and inner sides, thus they form ray like parenchyma. The new cambial segments constantly form the rays of parenchyma thus increasing in diameter. As the vascular cylinder, broken by wide rays, increases in circumference the cylinder of sclerenchyma that encircled the bundles becomes ruptured and adjacent parenchyma grows intrusively into the gaps. Eventually a very fluted vascular cylinder is formed. Species of *Aristolochia* are woody climbers or *lianas*, which have diverse taxonomic affinities and often shows anomalous structural features. Among other characteristic, the vessels are often of unusually wide diameter.

In *Bauhinia rubiginosa*, there is restriction of the activity of the cambium to certain regions which results in the formation of ridged stems. In other species of *Bauhinia*, the strap like stems are formed because of restricted activity of the cambium in certain regions. In this case, the cambium is more active at two opposite sides.

In some climbing plants (e.g., *Vitis*, *Clematis*), the interfascicular cambium forms only parenchyma, so that the original vascular bundles remain discrete throughout secondary growth.

Presence of Phloem Wedges in the Xylem. In *Bignonia unguis-catae* the young stems exhibit a normal ring of vascular bundles. However, during secondary growth, four furrows at four equidistant points appear in the xylem extending almost to the pith. The active cambium is situated on the inside of the furrows and produces large amounts of secondary phloem towards outside. The phloem increases in bulk, and the tissues slide along the lateral surfaces of the furrows. Later on, because of the development the furrows again become closed. The four radial groups of phloem are united by medullary ray tissue.

Formation of Interxylary or Included Phloem. The development of interxylary or included phloem takes place by means of the variation found in the activity of the cambium. The interxylary phloem is always secondary in nature and found in the form of strands (islands) which remain embedded in the secondary xylem. The development of included phloem has been studied in very few plants. In *Combretum*, *Entada*, *Salvadora*, and *Leptadenia*, certain small segments of the cambium cut phloem cells towards the inside of it for a short period of time, instead of cutting xylem cells, which are generally cut in normal conditions. After a short period, the cambium once again functions normally and cuts xylem cells inward instead of phloem cells in abnormal conditions. Thus inwardly formed phloem becomes embedded in the secondary xylem. This process is repeated several times, and the interxylary phloem patches are developed.

Accessory Cambium Formation and its Activity

In the stems of *Bougainvillea*, and other members of the Nyctaginaceae (e.g., *Boerhaavia diffusa*, *Mirabilis* etc.), several cambia arise successively in a centrifugal direction. Each cambium produces xylem and conjunctive tissue to the inside, and phloem and conjunctive tissue to the outside. The resulting tissue gives the appearance of concentric rings of vascular bundles embedded in conjunctive tissue.

A similar pattern of development is also observed in *Cycas* stem during secondary growth.

Extrastelar Cambium

In *Amaranthus*, *Achyranthes* and *Chenopodium*, the extrastelar cambium arises in the pericycle. In *Amaranthus* the cambium is found in the form of a complete ring, whereas in *Achyranthes*, it is represented by separate strips or arcs.

Secondary development in the monocots

Monocotyledons usually lack secondary growth from a vascular cambium but may develop thick stems (e.g., palms like *Roystonea* sp.) by a thickening growth

resulting from division and enlargement of ground parenchyma cells. This growth is called *diffuse secondary growth*.

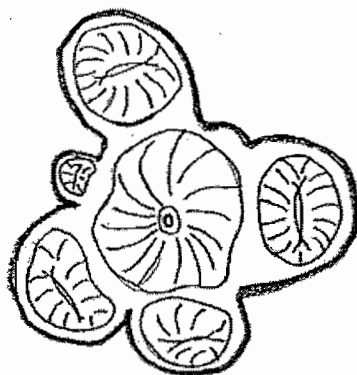
This primary growth of thickness in several monocots is due to a region of actively dividing meristematic cells called the primary thickening meristem that surrounds the apical meristem at the tip of a stem. In woody monocots, this meristematic region extends down the periphery of the stem where it is called the *secondary thickening meristem*.

Secondary growth by means of this special kind of cambium (*secondary thickening meristem*) occurs in herbaceous and woody Liliiflorae (*Agave, Aloe, Cordyline, Dracaena, Sansevieria, Yucca*) and other taxa. This cambium is continuous with the primary thickening meristem if the latter is discernible, but it functions only in the part of the stem that has completed elongation. The cambium arises in the parenchyma outside the primary vascular bundles and produces secondary vascular bundles and parenchyma toward the inside and a small amount of parenchyma toward the outside.

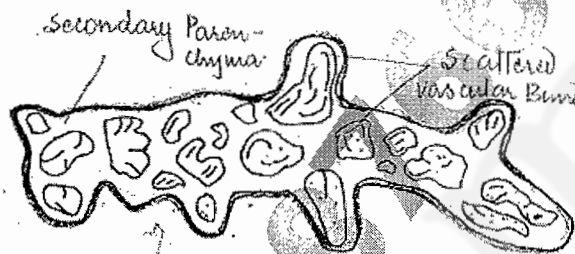
In the development of the vascular bundles, individual cells derived from the cambium divide longitudinally; then two or three of the resulting cells repeat the longitudinal divisions. The products of the final divisions differentiate into vascular elements and associated sclerenchyma cells. Vertically, many tiers of cells combine to form a vascular bundle. The secondary vascular bundles may be collateral or amphivasal and occur in more or less definite radial files. Some monocotyledons form the type of periderm found in dicotyledons (*Aloe, Cocos, Roystonea*); others have the so-called storied cork as a protective tissue.

Illustrations on anomalous secondary growth

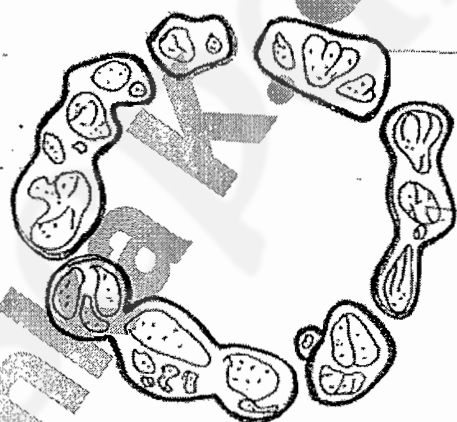
I. UNUSUAL POSITIONING OF THE CAMBIUM.



T.S. - through stem of Thinnocia scandens showing anomalous secondary growth.



T.S. Through stem of Bauhinia longispina.



T.S. Through stem of Serjania ichthyocarpa showing anomalous secondary growth.

ABNORMAL DIVISION PATTERN IN CAMBIUM.

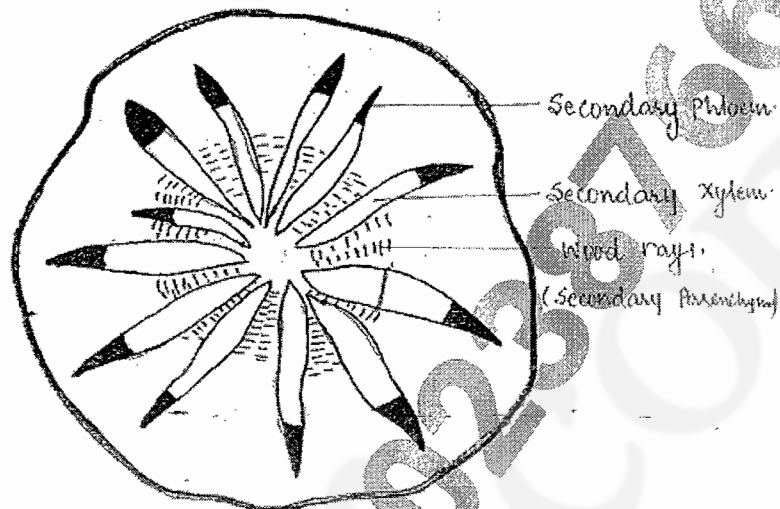


Fig: T.S. Through the stem of Aristolochia showing abnormal sec. growth.
(same pattern also seen in Urtica, Urtica & Begonia fruticosa)

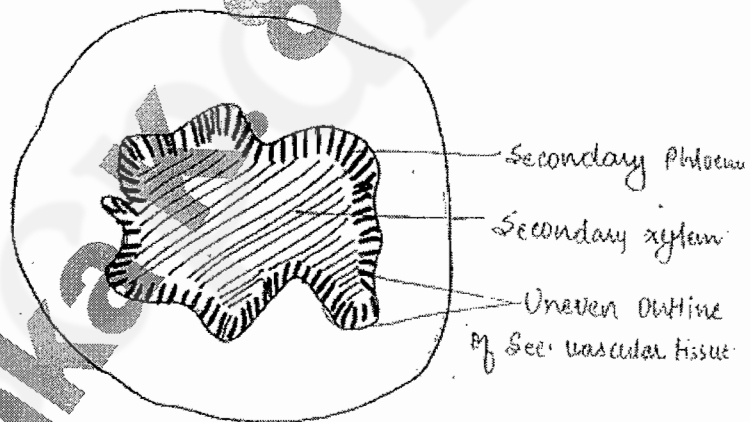


Fig: T.S. Through stem of Benthonia subginnosa.

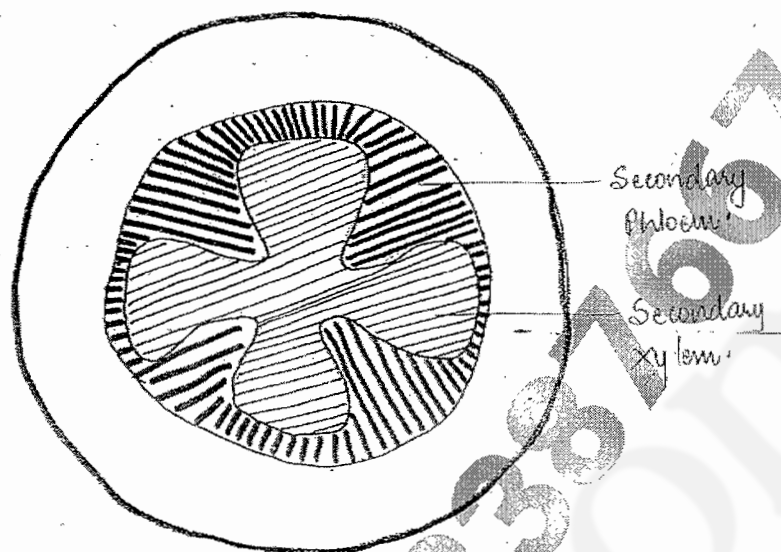


Fig: T.S. stem of Bignonia imbricaria (The stage after secondary growth)

III.

PRESENCE OF MULTIPLE CAMBIA

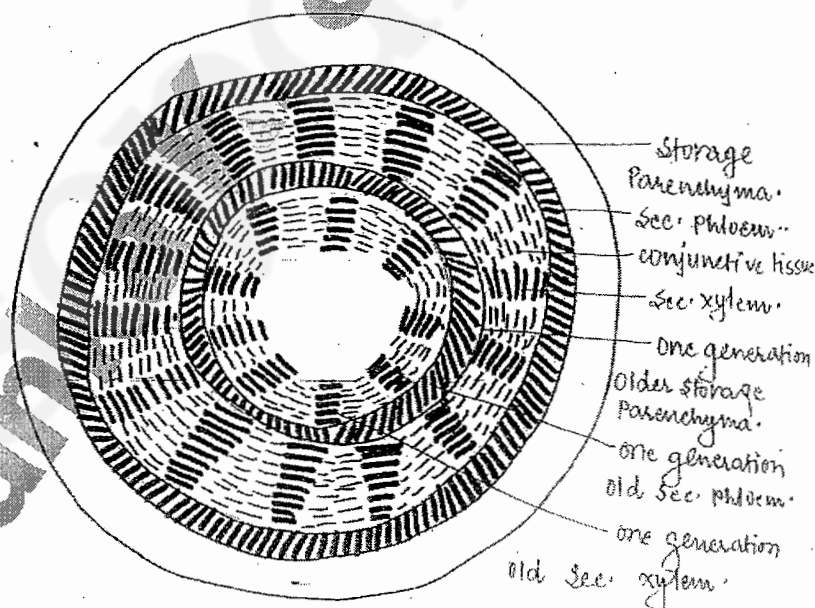


Fig: T.S. stem showing multiple cambia (Schematic).

IV. EXTRA-STELAR CAMBIUM

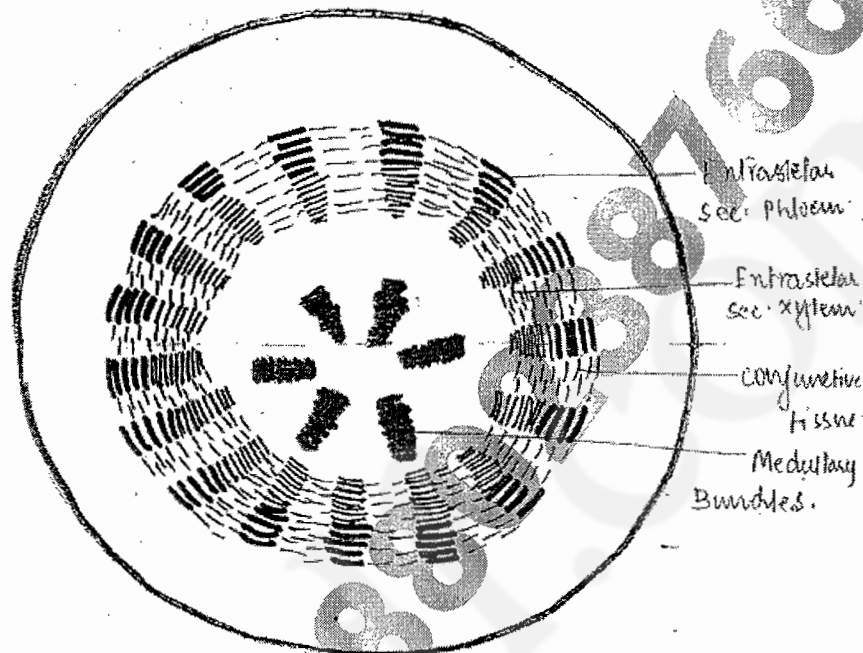


Fig: T.S. stem showing extra stelar cambium in Pericycle (schematic).

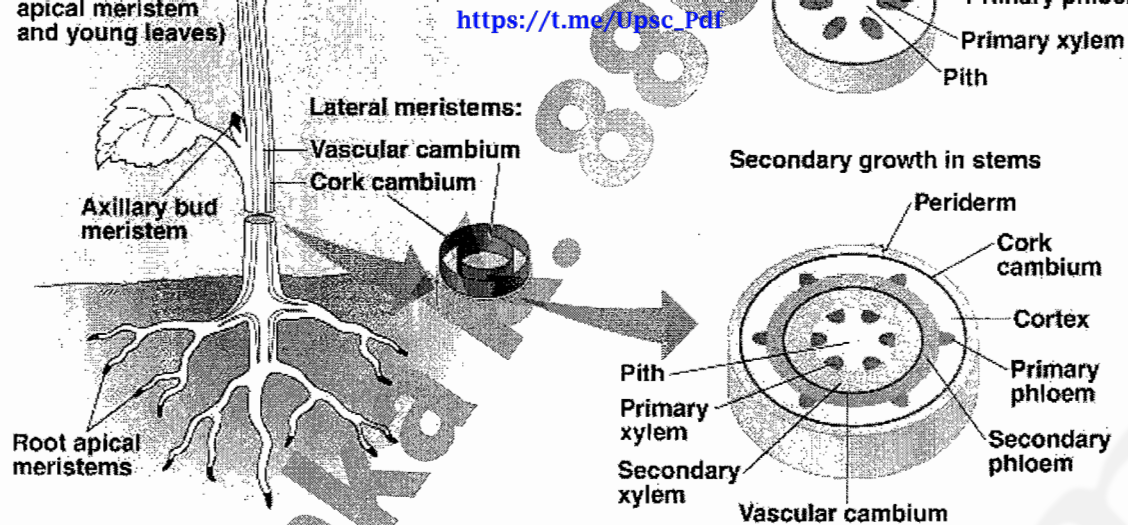
Best studied cases are:

(a) *Amaranthus* sp.

(b) *Chenopodium* sp.

apical meristem
and young leaves)

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